

FEEDING ACTIVITY, ENERGY BALANCE AND SCOPE
FOR GROWTH IN THE JUVENILE SEA SCALLOP
PLACOPECTEN MAGELLANICUS (Gmelin)
IN NEWFOUNDLAND

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FEEDING ACTIVITY, ENERGY BALANCE AND
SCOPE FOR GROWTH IN THE JUVENILE SEA SCALLOP

PLACOPECTEN MAGELLANICUS (Gmelin)

IN
NEWFOUNDLAND

BY

© GREGORY S. BACON

A thesis submitted to the School of Graduate
Studies in partial fulfilment of the
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Master of Science

Department of Biology
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St. John's

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Abstract

The physiological responses of juvenile sea scallops (Placopecten magellanicus) (Gmelin.) exposed to experimental food rations, that varied in concentration and quality, were evaluated using techniques of physiological energetics. This included: 1) the pre-ingestive feeding activity such as clearance rate, pseudofaeces production and preferential selection; 2) energy gained through ingestion and absorption; 3) energy losses associated with respiration and excretion; and 4) the integration of these energy gains and losses to predict scope for growth.

To accomplish this, scallops were exposed to laboratory experimental diets with qualities (at 12° C) set at 25%, 50%, and 80% particulate organic material (POM) and diet concentrations set at approximately 1, 3, 7, and 14 mg l⁻¹ using varying proportions of the microalgal diatom Chaetoceros muelleri and inert silica particles (SiO₂). These conditions mimicked the range of seston conditions this species is exposed to in the natural environment in eastern Newfoundland.

Juvenile sea scallops exposed to the above conditions were able to regulate ingestion rate by reducing clearance rate and increasing the amount of material rejected in pseudofaeces, all in order to maintain a high absorption

efficiency. An increase in scope for growth by this species with particle concentration was facilitated by maintaining relatively constant oxygen consumption and ammonia excretion rates.

P. magellanicus showed no relative difference in scope for growth at concentrations greater than 3 mg l⁻¹ when fed a 50% organic mix of algae and silica when compared to a ration consisting of 80% organic content (i.e. 100% algae). A direct grow out experiment would be required to confirm that scallops could grow as effectively on a 50% diet as on an 80% diet, but these results suggest the cost of rearing algae and the hatchery/nursery stage of culturing this species of scallops could be reduced by supplementing algal food with inorganic particles such as silica.

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1. Introduction

The sea scallop, Placopecten magellanicus (Gmelin), is a benthic bivalve found only in the Northwest Atlantic from the north shore of the Gulf of St. Lawrence to Cape Hatteras, North Carolina (Posgay 1957, Porter 1974). P. magellanicus is the most economically important pectinid species in the world, contributing between 30 and 50% of the annual global scallop production (Naidu 1991). The sea scallop supports a large fishery on the east coast of North America, representing a total value in Atlantic Canada of \$55 million in 1988 (Anon, 1989). Uncertainty in the future of these stocks and a strong North American market with high prices has prompted a great deal of interest in studying factors that influence survival and regulate growth rates in this species. A better understanding of how environmental factors affect scallop growth and production is necessary to determine how fast juveniles are recruited into the fishery or how rapidly they can be harvested from aquaculture farms.

One of the major factors influencing growth rates in the sea scallop is the availability of food in the natural environment (MacDonald and Thompson 1985). Like other suspension-feeding bivalves, scallops filter suspended particles such as phytoplankton, detrital material and sediment from the surrounding water to gain nutrition and support growth. Establishing the relationship between the

food supply and growth rate requires a knowledge of the animal's feeding capabilities over a wide range of natural conditions. This includes rates of particle uptake, size of particles retained, and the efficiency of absorption. A better understanding of how P. magellanicus exploits its food resource and its adaptability to particular habitats may assist aquaculturists with the selection of the most appropriate aquaculture sites for growout or in the selection of optimal diet levels for the hatchery nursery stage.

1.1 Energy balance and scope for growth:

Techniques of physiological energetics are often used to integrate measurements of energy gain and loss under varying food and temperature conditions into an overall index of energy balance. This enables the physiological and behavioral response of organisms to different conditions to be assessed and predicts the energy potentially available for growth and gamete production, referred to as "scope for growth" (Warren and Davis 1967, Bayne and Newell 1983). The animal's ability to adjust its physiological activity under different circumstances must be taken into consideration when estimating energy gain through feeding activity and energy loss through maintenance metabolism. This approach

provides an alternate method to time consuming growout studies for assessing growth responses.

Energy balance in an organism is described by the equation:

$$C = P + R + F + U$$

where C = energy gained through consumption, F = energy loss in faeces, U = energy loss in excretory products (i.e. ammonia), R = respiratory heat loss and P = energy invested in the production of soma and gametes (Vahl 1981, Bayne and Newell 1983). By rearranging this equation it is possible to calculate several parameters relevant to energy balance such as the absorbed ration (AB). For example, $AB = C - F$ or $AB = C \times AE$, where AE is absorption efficiency (Thompson and MacDonald 1991). Scope for growth has also been referred to as the assimilated ration (A) or the physiological useful ration and is estimated using this equation (Bayne and Newell 1983):

$$A = AB - (R - U)$$

Factors that influence energy gain in bivalves are clearance rate, rate of pseudofaeces production and the efficiency of absorption. Clearance rate is the volume of

water cleared of suspended particles (greater than $2.0\ \mu\text{m}$) per unit time (Bayne et al. 1977). Pseudofaeces production is the amount of material cleared from suspension but rejected prior to ingestion per unit time. Absorption efficiency is the proportion of organic material extracted from the seston (suspended particulate matter) (Conover 1966).

Energy losses associated with maintenance metabolism are estimated by measuring respiration and ammonia excretion rates. Maintenance, in this context, represents energy lost to respiration plus such factors as gametogenesis and the cost of digestion. Respiration rate represents the proportion of energy intake (or of available body reserves) required to support life processes (Widdows 1985). Energy losses by respiration can be expressed in terms of oxygen consumption, carbon dioxide liberation or heat production, including any anaerobic component. Respiration rates in bivalves are commonly measured as oxygen consumption because energy loss in the form of heat, resulting from biochemical oxidation and various motor activity, is generally regarded as impractical to measure routinely on small animals (Widdows 1985). Nitrogenous excretion rates are not commonly measured directly because bivalves are primarily ammonotelic and nitrogenous losses usually represent a small component of the energy budget (i.e. less than 5 % in the sea scallop

P. magellanicus (Thompson 1984)). However, excreted nitrogen may constitute a significant metabolic loss for some species such as the blue mussel (Bayne and Scullard 1977).

1.2. Energy gain through feeding activity.

In the natural environment bivalves are exposed to a food supply that fluctuates in both quantity and quality, and face a major adaptive challenge in supporting growth and reproduction, especially when the food supply is poor. Despite some recent studies on feeding activity (Shumway et al. 1985, MacDonald and Thompson 1986, Cranford and Grant 1990, Ward et al. 1992) there is relatively little information available on the ability of P. magellanicus to exploit a food supply that varies in concentration and quality.

Many studies have examined feeding responses and energy balance in bivalves using diets of monocultured algae with little refractory or inorganic material. These studies focused on feeding and growth responses due to variation in the quantity of the diet, often at food concentrations much higher than those experienced by the bivalve in the field. Only recently have authors examined the effects of increasing food quality, at concentrations near natural seston levels, on energy balance and feeding behaviour (e.g. Bayne et al. 1987, 1989; Iglesias et al. 1992).

When exposed to increasing suspended particle loads bivalves are able to regulate or control the total amount of material ingested by a) reducing the time spent pumping, b) reducing their clearance rate and or c) increasing the amount of material rejected in pseudofaeces (Foster-Smith 1975, 1976).

Clearance rates rise with increasing particle concentration at relatively low levels, reach an asymptote at intermediate concentrations, and then decline at very high experimental concentrations (Bayne and Newell 1983). However, ingestion rates generally increase rapidly with seston concentration before becoming independent of concentration at intermediate and high seston levels (Bayne and Newell 1983). Clearance rate in P. magellanicus increases with increasing seston quality (Cranford and Grant 1990, as does ingestion rate in bivalves (Bayne et al. 1989 and Cranford and Grant 1990). It is difficult to compare these studies directly or describe trends that apply to bivalves in general because there were many differences among the species used, techniques employed, and the concentrations and qualities of the particles that compose the experimental rations.

Regulation of clearance rate and the amount of time spent feeding can only alter the amount of material ingested. The production of pseudofaeces can alter both the

amount and the quality of the material to be ingested. For example, it can prevent particle overload and eliminate excess material that exceeds the ingestive capacity of the bivalve and simultaneously allow the rejection of poorer quality particles, thereby improving the quality of ingested material (Kjørboe and Møhlenberg 1981, Newell and Jordan 1983, MacDonald and Ward 1994). Pseudofaeces production typically increases with particle concentration after a threshold concentration has been exceeded (Bayne and Newell 1983). If bivalves have the ability to reject poorer particles preferentially, they may be able to counteract the "dilution effect" observed when seston concentrations increase disproportionately in the particulate inorganic matter (PIM) (Widdows et al. 1979). The possibility of preferential selection should be taken into consideration in any analysis of bivalve feeding behaviour (Bayne et al. 1988).

Any pseudofaeces production must be taken into account in the energy budget equation above when calculating the ingestion or consumption rate

$$I = (CR \times B) - PS$$

where I is the ingestion rate, CR is the clearance rate, B is the food concentration and PS is the rate of pseudofaeces production (Malouf and Bricelj 1989).

Recent studies suggest that the relationship between food conditions and absorption efficiency observed for scallops does not differ markedly from that for other bivalves (Bricelj and Shumway 1991). Absorption efficiency decreases with increasing algal concentration in Mercenaria mercenaria and Mytilus edulis, but at natural particle concentrations no increase occurs (Bayne and Newell 1983, Bricelj and Malouf 1984). As in other suspension feeding bivalves, a scallop's absorption efficiency decreases with increasing food concentrations (Bricelj and Kuenster 1989). Absorption efficiency increases in M. edulis, at a reducing rate, with increasing seston quality (organic material) (Bayne et al. 1987, 1989). Absorption efficiency has also increased in P. magellanicus fed increasing POM levels in sediment diets (Cranford and Grant 1990), and has been inversely related to the fraction of inorganic matter in the seston for Chlamys islandica (Vahl 1980).

Scope for growth, expressed in terms of carbon and nitrogen units, was recently described for P. magellanicus by Grant and Cranford (1990). They exposed scallops to a variety of diets such as kelp debris, phytoplankton and resuspended sediment and found that kelp could enhance

growth in phytoplankton diets but could not act as a sole food source (Grant and Cranford 1991).

Experiments using single species of microalgae have found increases in scope for growth in mussels fed increasing algae concentrations (Thompson and Bayne 1974, Griffith and King 1979). Other authors have examined the effect on growth of non-algal supplements in food such as yeast, rice starch and cheese whey (Urban and Langdon 1984). When fed natural seston mixtures (instead of single algal diets), bivalves typically have displayed an increase in scope for growth with increasing seston quantity (Widdows 1978, Stuart 1987, Bayne et al. 1989). In terms of seston quality, scope for growth in bivalves either increases with increasing quality (Grant and Cranford 1991) or shows little change with increasing quality (Bayne et al. 1989).

1.3 Energy losses through respiration and excretion.

Respiration rate, measured by the rate of oxygen consumption, is influenced by a number of variables, including temperature, body size, oxygen tension, reproductive state, salinity, activity level, physiological condition and food concentration. A common response during periods of low food availability in bivalves is a reduction in the rate of oxygen consumption (Bayne 1973, Calow 1977). Vahl (1980) measured oxygen consumption in C. islandica and

found that the seasonal variations in the food supply over the year explained the variation in oxygen consumption better than changes in temperature. MacKay and Shumway (1980) found that feeding did not effect the respiration rate (oxygen consumption) in the deep water scallop C. delicatula and they suggested that discontinuous feeders, such as scallops, may respond to changes in the food supply in terms of their respiration rates more noticeably than species that feed continuously. Studies on the effects of environmental factors or physiological condition on respiration rates have provided a wide variety of results especially for the well studied marine mussel, Mytilus edulis. For example, this species has been found to maintain its rate of oxygen uptake with changes in particle concentration (Widdows et al. 1979) and seston quality (Thompson 1984, Bayne et al. 1987, 1989), to display high metabolic rates even at low temperatures, which is probably related to their gametogenic condition (Widdows and Bayne 1971; Gabbott and Bayne 1973) and to increase its oxygen uptake exponentially with increased rates of absorption (Bayne et al. 1989).

Changes in rates of nitrogen excretion are often related to overall metabolic losses by means of oxygen: nitrogen ratios (Bayne and Newell 1983). Some studies, however have specifically related ammonia excretion rate to

changes in seston quantity and quality. Grant and Thorpe (1991) found an increase in ammonia excretion rate through time in turbidity experiments with Mya arenaria. However, ammonia excretion in M. edulis has also shown little change with increasing seston quality (Bayne et al. 1987).

1.4 Objectives.

The objective of my study was to evaluate the following physiological responses of juvenile sea scallops (Placopecten magellanicus between 40-50 mm shell height) exposed to experimental rations that varied in concentration or quality:

- (1) the pre-ingestive feeding activity (clearance rate, pseudofaeces production, preferential selection),
- (2) energy gained through ingestion and absorption
- (3) energy losses associated with respiration and excretion
- (4) the integration of these values to derive the scope for growth.

Scallops were exposed to laboratory experimental diets representative of the range of seston conditions experienced in the natural environment in eastern Newfoundland. For example, in this habitat seston concentrations range from 2-15 mg l⁻¹ and organic composition typically varies from 20-50% depending on the season (MacDonald and Thompson 1986).

Diet qualities (at 12° C) were set at 25%, 50% and 80% POM and diet concentrations set at approximately 1, 3, 7, and 14 mg l⁻¹ by varying the proportions of microalgae (pure diatom culture) and silica particles. The 80% diet exceeded levels found in nature (MacDonald and Thompson 1986). However, exposure to this level of POM (pure microalgae) provided the opportunity to assess the scallops response to artificially high levels and to compare this study to many published reports that used only cultured algae.

Gaining a better understanding of how environmental factors affect the sea scallop, how P. magellanicus exploits its food resource, and its ability to adapt to particular habitats, may assist aquaculturists with the selection of the most appropriate aquaculture sites for growout or in the selection of optimal diet levels for the hatchery nursery stage.

2. Materials and Methods

2.1. Experimental Conditions

2.1.1. General Measurements

Juvenile sea scallops (Placopecten magellanicus (Gmelin), obtained from spat collectors and held under culture conditions, were supplied by Thimble Bay Farms in Notre Dame Bay, northeastern Newfoundland. Scallops were acquired at bimonthly intervals between October 1990 and January 1991. All experiments were conducted in the Laboratory at the Ocean Sciences Centre, Logy Bay, Newfoundland.

To reduce potential variation in physiological estimates that may be attributable to differences in body size, only scallops from 40-60 mm in height were used. All scallops were held in the laboratory in flowing unfiltered seawater at constant temperature, $12^{\circ}\text{C} \pm 1^{\circ}\text{C}$. Recently collected animals were acclimated to $12^{\circ}\text{C} \pm 1^{\circ}\text{C}$ for two weeks, the temperature used for all physiological experiments. Scallops were held from a minimum of two weeks to a maximum of eight weeks before being used in an experiment.

Weights of gonad and remaining body tissue (somatic) and shells (tissue removed) for individual scallops were

obtained to the nearest 0.01 g, after drying at 80° C for 72h. Shell length and height were recorded to the nearest 0.1 mm using vernier callipers. Shell height is the maximum distance between dorsal and ventral margins when considering the hinge to be dorsal in position (Seed 1980).

2.1.2. Experimental Diet Mixtures

Scallops were exposed to four experimental diet concentrations (1, 3, 7, and 14 mg dry weight l⁻¹). Dietary quality was set at either 25, 50 or 80 % particulate organic matter (POM) (ash free dry weight; AFDW) for each of the four concentrations, resulting in 12 different experimental combinations. Diets consisted of mixtures of the micro algae Chaetoceros muelleri, silica and filtered sea water. C. muelleri was grown in autoclaved f/2 medium, at 20° C, under constant illumination (fluorescent cool white lights) and was bubbled with filtered air. Microalgal growth was monitored daily and cultures were harvested for use when they were approximately at their exponential growth phase. Silica is considered inert and constituted the majority of the inorganic fraction of a diet. In a preliminary experiment, individual weights (\pm 0.01 mg) and % particulate organic material (POM) of the microalgae and silica were estimated separately by filtering known quantities of each

onto pre-weighed Whatman GF/C filters (2.5 cm diameter) and weighing them on a microbalance. Calculations of concentration and quality of each diet in mg l^{-1} and % POM were based on different proportions of the organic and inorganic fractions (see Appendices A.1., A.2., A.3.).

2.1.3. Particle Size Distributions

The particle size range of each diet fed to the scallops was monitored using a Coulter Multisizer (Model II) fitted with a 100 μm orifice tube. The silicon dioxide purchased from Sigma chemicals had a predetermined size range of between 1.0 and 10.0 μm with 80% of the silica between 1.0 and 5.0 μm . This size range was similar to that of the alga Chaetoceros muelleri ($\approx 4\text{--}6$ μm in diameter), used to make up the organic fraction of the diet. (see Appendix B, Figure B.1.). Thus, if preferential selection was demonstrated by the scallops, this would illustrate their ability to select based on the quality of the food particle rather than just its size. All size distributions were saved on computer disk for later analysis and expressed as particle number or volume versus log particle size classes using Coulter Multisizer AccuComp Color Software (Coulter 1989).

2.1.4 Standardization of Physiological Rates.

To compare metabolic and clearance rates for different groups of experimental scallops it was necessary to correct for weight differences among scallops of similar shell height. Therefore, physiological rates were converted to a "standard" animal of 1 g tissue weight using the following equation:

$$Y_s = (W_s / W_e)^b \cdot Y_e$$

where: Y_s = the physiological rate for an animal of standard weight, W_s = the standard weight of the animal, W_e = the observed weight of the animal, Y_e = the uncorrected (measured) physiological rate, b = the weight exponent for the physiological rate function. Weight exponents used were those calculated for P. magellanicus in Newfoundland by MacDonald and Thompson (1986). Seven scallops were used for each experiment or diet. Each scallop was numbered so that its individual physiological rate could be analyzed later.

2.2. Estimating Energy Uptake

2.2.1. Clearance Rate

2.2.1.1. Acclimation to Diet

Prior to use scallops were maintained on a batch fed diet of about one litre per day of C. muelleri per seven scallops. The scallops were exposed to the specific experimental diet for 24h before physiological rates were measured. All sea water was pre-screened through a 100 μm , a 10 μm and a 1 μm in-line filter cartridge to reduce potential variations in experimental diets associated with fluctuations in the natural seston in the incoming seawater supply. To obtain the desired concentration and quality of diet, separate slurries of algae and silica were pumped to the feeding apparatus using a multi channel peristaltic pump. Algal slurries were gently bubbled using an air stone, and silica mixtures were stirred by submersible, stirrers to prevent particles from settling out.

2.2.1.2. Determination of Diet Concentration and Quality

To verify the concentration and percent POM of the experimental diets, water samples from the overflow hose on the mixing bucket were collected on the day clearance rates were determined (see clearance rate experiment, section 2.2.1.4. below). The positioning of the hoses containing

incoming sea water and food in the mixing bucket, plus adequate stirring, ensured equal volumes of diet mixture were supplied to scallops and the overflow hose simultaneously (see clearance rate experiment, section 2.2.1.4. below). Water samples collected were measured at a volume appropriate for weight determination. For example, if the particle concentration was relatively low, a large volume had to be collected to obtain an accurate dry weight in mg l^{-1} . The bucket was plunged with a clean plunger to ensure adequate mixing before the sample was divided into four replicates of equal volume.

Samples of seawater were collected at the beginning, middle and end of the clearance rate experiment. A minimum of two litres for the 14 mg l^{-1} diets and a maximum 32 litres for the 1 mg l^{-1} diets was collected to ensure there would be adequate material on the filter for weight determination. Each sample was thoroughly mixed and divided into four replicates. The Multisizer was used to determine the number and size distribution of particles from a 250 ml sub-sample. A total of 16 samples were collected for each diet, four replicates for the blanks and four replicates each of the diet time series.

A sample of each diet mixture was collected by filtering the seawater through pre-ashed, pre-weighed

Whatman GF/C filters (4.5 cm diameter) under low vacuum. Each replicate above was filtered onto a separate filter. All filters were washed with 10 ml of isotonic ammonium formate prior to drying to constant weight at 80° C.

2.2.1.3. Filter Processing and Energy Content

The amount of particulate organic matter (POM) and inorganic matter (PIM) in each diet was determined from eight of the above replicate filters (two sea water blanks; two diet sample filters from each of the three collection times). Filters were dried to constant weight at 80° C, weighed, combusted at 450° C for 12 hours and reweighed after cooling in a desiccator. The ash free dry weight and thus the % POM for each diet (after the sea water blank had been subtracted) was determined from the mean of the above values.

Estimates of the quality of the food available were obtained from the energy content (wet oxidation) or the concentration of carbon and nitrogen in the suspended particulates (CN analysis).

Wet oxidation has commonly been used to estimate energy content by converting oxygen demand of the organic content to energy values using a conversion factor (Elliot and Davison 1975). The wet oxidation technique described by

Newell (1982) was used in my study. Known weights of seston on glass filters were oxidized to their basic elements using a known volume of a strong oxidizing agent, 2N potassium dichromate in concentrated sulphuric acid. The amount of oxidant reduced was determined by titrating dichromate on the filter against an $\approx 0.75N$ ferrous sulphate solution. The weight of oxygen (O.C mg) required for complete oxidation of the organic matter was calculated using the following equation: $O.C = (A-B) \times N \times 8$ where A is the volume (ml) of the ferrous sulphate required to titrate the blank, B is the volume (ml) of ferrous sulphate required to titrate the sample, N is the normality of the ferrous sulphate and 8 is the equivalent weight for oxygen. The energy content (Joules) of a sample can then be calculated by multiplying O.C by 14.14 (Newell, 1982). The energy content in $J\ filter^{-1}$ was divided by the total weight of a sample to obtain weight specific energy content ($J\ mg^{-1}$).

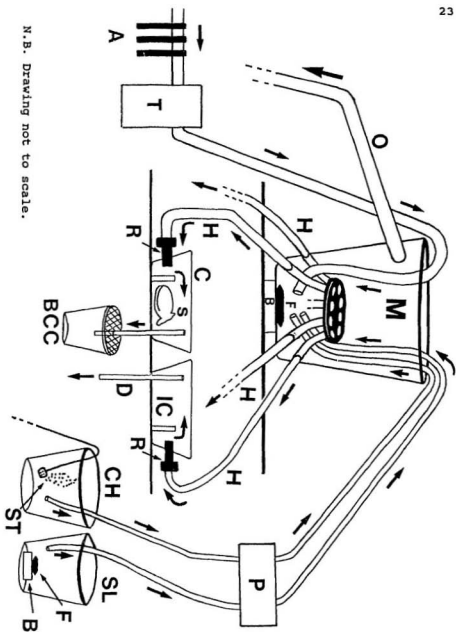
Concentrations of particulate organic carbon (POC) and nitrogen (PON) were determined by combustion in an oxygen atmosphere using a Perkin-Elmer CHN Elemental Analyzer (Model 2400). Diet quality was expressed as μg of carbon and nitrogen per mg dry weight of seston.

2.2.1.4. Clearance Rate

Clearance rate (CR) is a measure of the feeding activity of a scallop and is defined as the volume of the water cleared of suspended particles $\geq 2 \mu\text{m}$ in diameter per unit time (Bayne et al. 1977). Scallops were exposed to the appropriate experimental diet for 48 hours prior to the measurement of feeding rates. The apparatus (Figure 1) consisted of a seawater line equipped with an in-line cartridge system consisting of a coarse, a $10 \mu\text{m}$ and a $1 \mu\text{m}$ filter in a sequence, a temperature control unit, a 20 l mixing bucket or constant volume header tank. Separate slurries of C. muelleri and silica were pumped to the mixing bucket by a peristaltic pump at a rate calculated to supply the desired experimental diet. Both the silica slurry and the experimental diet in the mixing bucket were stirred by submersible stirrers and stir bars. The algal slurry was bubbled with an air stone. Scallops were placed individually in one litre plastic containers with flow restrictors supplying known volumes of suspension to the containers via plastic hoses from the mixing bucket. One container was left empty serving as the inflow control. Inflow to the mixing bucket was sufficient that water flowed continuously through the overflow, thereby providing a constant head which ensured that the flow through each hose varied less than 10%. Preliminary testing of the system ensured that equal

Figure 1. Clearance Rate Flow-Through Apparatus
Arrows indicate direction of water and diet mixture flow through the hoses and the apparatus.

Legend: A: sea water filter cartridges
B: submersible stirrer
BBC: biodeposit collector cup
C: 1 l plastic container
CH: bucket of C. muelleri
D: drain
F: stir bar
H: pvc hose
M: 20 l mixing bucket
O: over flow hose from mixing bucket
P: peristaltic pump
R: flow restrictor
S: scallop
SL: bucket of silica
ST: air stone/bubbler
T: Temperature control unit



N.B. Drawing not to scale.

volumes of diet mixture were supplied to each container simultaneously (see Appendices C, C.1.). Flow rates of 150-180 ml min⁻¹ were used because it was determined that CR was independent of water flow in this range (see Appendices C, C.2.). Once water passed through the flow restrictor it was delivered to the bottom of the container via a plastic hose to the scallop. A plastic baffle at the front of the scallop container ensured adequate mixing of the suspension in the container. The size and shape of the oblong containers (C) prevented any recirculation of the diet mixture. All scallops were secured to the bottom of the container using velcro (fabric end glued to right valve with water resistant epoxy) with the excurrent portion of the mantle positioned adjacent to the drain. Water then flowed into plastic biodeposit collector cups fitted with 80 μ m mesh to minimize loss of faeces or pseudofaeces.

The duration of the CR experiment for each diet condition was approximately seven hours, to allow adequate time for scallops to acclimate to the containers and reach a steady state of feeding. Water samples from the overflow drains of scallop and control containers were collected simultaneously approximately every 1.5 hours over a period of one minute to three minutes allowing the flow rate to be determined. The number of particles in suspension was

determined with a Coulter Multisizer (Model II) fitted with a 100 μm tube. The clearance rate was calculated according to Bayne et al. (1977) as follows:

$$\text{CR} = \text{FR} \times \left(\frac{\text{C}_1 - \text{C}_2}{\text{C}_1} \right)$$

where CR is the clearance rate in litres h^{-1} , FR is the flow rate of water through the containers (litres h^{-1}), C_1 is the particle concentration (counts ml^{-1}) in the inflowing water (determined from the control container) and C_2 is the particle concentration (counts ml^{-1}) in the outflowing water. The final clearance rate for each scallop was the mean of a minimum of three consecutive and consistent rates measured over the experimental period. This was termed active clearance rate. A second clearance rate for each scallop was also calculated and was the mean of all rates over the experimental period. This second rate was termed the routine clearance rate and included periods when the scallop was not feeding.

2.2.1.5. Collection of Biodeposits

Biodeposits were collected by a micro-pipette at the end of the experiment from both the containers and the plastic cups and placed in vials. Faeces and pseudofaeces

were collected separately and were clearly distinguishable. Faeces formed small pellets and sank to the bottom of the container, whereas pseudofaeces formed fixed clumps and tended to float in the cups. Pseudofaeces were placed in glass vials with one or two drops of 5% formalin (v/v) and stored in the dark at 6° C to prevent cell decomposition. Faeces samples were stored at -20° C until processed. An equivalent volume of biodeposit free water was collected from each scallop container as a control. All scallops were returned to the holding tank and fed the respective experimental diet until the ammonia excretion experiment the following day (see Experimental Schedule section 2.3.).

2.2.2. Pseudofaeces

Each individual pseudofaeces sample was processed in the following manner: excess water was carefully pipetted out of each vial leaving approximately 20 ml to which one drop of nonionic dispersant was added. The sample was then sonicated for one minute. Each vial was shaken well and the contents rinsed carefully through a 100 µm screen, poured into a Coulter cuvette and made up to a constant volume with filtered sea water. The exact volume was then measured in a graduated cylinder and the complete sample transferred back to the same cuvette.

The total number of particles in each pseudofaeces sample (ml^{-1}) was estimated with a Coulter Multisizer. If coincidence was too high (probability that two or more particles will pass through the aperture simultaneously, $>10\%$) samples were diluted with filtered seawater. Individual samples were then filtered onto 2.5 cm GF/C pre-ashed, pre-weighed filters and rinsed with ≈ 5 ml of isotonic ammonium formate. If pseudofaeces amounts were excessive, samples were divided into subsamples before filtering and the weight and total count (particles ml^{-1}) combined afterward. A control was processed as above to serve as a background for particle count and weight. All samples were dried to constant weight at 80°C , weighed, combusted at 450°C and reweighed to the nearest 0.01 mg.

The following routine and active rates were measured or calculated for a standard 1 g scallop; (a) total particles cleared $\text{h}^{-1} \text{g}^{-1} = \text{CR} (\text{ml h}^{-1}) \times \text{diet concentration (particles ml}^{-1})$, (b) total pseudofaeces production or number of particles rejected $\text{h}^{-1} \text{g}^{-1}$, (Note that this quantity is independent of clearance rate and therefore does not have an active and routine value) (c) total particles ingested $\text{h}^{-1} \text{g}^{-1} = \text{total particles cleared} - \text{total particles rejected as pseudofaeces production}$, (d) percent of cleared particles

rejected in pseudofaeces = (total pseudofaeces
production/total particles cleared) X 100.

2.2.2.1. Selection Process

When pseudofaeces are produced, the scallop may alter, through preferential rejection of poorer quality particles, the organic content (POM) and hence the quality of the ingested diet (Kjørboe and Møhlenberg 1981, Newell and Jordan 1983). If POM in the pseudofaeces is significantly different from that of diet, then selection has occurred. This will invalidate the estimate of absorption efficiency, because the Conover ratio procedure assumes no selection (see Section 2.4.1.2. below). The concentration and percent POM recorded for the different diets were used to calculate the following estimates of feeding activity;

- (a) total amount cleared (mg) = routine CR ($l\ h^{-1}$) X
diet conc. ($mg\ l^{-1}$) X length of experiment (hs),
- (b) total amount ingested (mg) = total amount cleared
(mg) - total pseudofaeces (mg),
- (c) amount of POM cleared (mg) = total amount cleared
(mg) X percent POM,
- (d) total amount of POM ingested (mg) = amount of POM
cleared (mg) - amount of POM in pseudofaeces
(mg),

(e) percent organic ingested = amount of organic
 ingested (mg)/ total amount ingested (mg) X 100.

The percent enhancement or percent improvement (i.e. how much the scallop improved the ingested ration through selection) for each scallop that produced pseudofaeces was calculated by the following equation:

$$\frac{POM_{\text{ingested}} - POM_{\text{diet}}}{POM_{\text{ingested}}} \times 100$$

where POM_{ingested} is the total percent POM ingested and POM_{diet} is the percent POM of the diet. Routine rather than active clearance rates (Section 2.2.1.4.) were used to calculate enhancement because pseudofaeces were collected throughout the entire experiment and total pseudofaeces production corresponds closely to the total routine clearance rate over the same time period.

With the exception of the pseudofaeces values used to calculate percent enhancement, all values for pseudofaeces production that were calculated in mg h^{-1} were taken into account in the calculation of ingestion rate (mg h^{-1}) (Section 2.2.3. below), absorbed ration (Section 2.4.1.3. below) and scope for growth (Section 2.5. below). Active and routine clearance rates were used to calculate active and routine rates for ingestion (mg h^{-1}) and scope for growth (J

h⁻¹). Pseudofaeces production was standardized to 1 g dry tissue weight using the weight exponent of 0.68 for clearance rate from MacDonald and Thompson (1986).

Pseudofaeces production at the highest food concentrations (14 mg l⁻¹) was much greater than at the lowest (1 and 3 mg l⁻¹). Pseudofaeces production estimates at high concentrations are considered to be minimum estimates because pseudofaeces are very buoyant and some may have been lost through the small opening between the standpipe and the 80 μ m mesh of the biodeposit collector. More complete collection of pseudofaeces was obtained, however, for the low food concentrations because virtually all of the pseudofaeces stayed in the scallop containers. Scallops from two of the diets produced no pseudofaeces (1 mg l⁻¹ 80 % and 3 mg l⁻¹ 25 % POM).

The slope for the regression of pseudofaeces production vs percent POM in the diet (for diets where all the pseudofaeces were collected) was not significantly different from zero ($T = -1.82$, $P = 0.0738$, $r^2 = 0.052$). Therefore, pseudofaeces production, at least at lower concentrations, was independent of percent POM. Pseudofaeces data from diets where all the material was collected were therefore grouped and regressed against food concentration. This produced a simple linear regression equation: $Y = 0.99(\text{diet conc.}) -$

1.04 , where Y is the pseudofaeces production (mg). The slope for this equation was significantly different from zero ($T = 10.94$, $P = 0.0001$, $r^2 = 0.666$). The predicted mean pseudofaeces production for the high concentration diets was then extrapolated from this equation. These values, together with the organic content of the pseudofaeces, were used to calculate ingestion rates, absorption efficiency and scope for growth.

2.2.3. Ingestion Rate

Ingestion rate is defined as the amount of material cleared from suspension minus the amount of material rejected as pseudofaeces per unit time (mg or mg h^{-1} or particles h^{-1}). Ingestion rate was calculated as the product of the CR (l h^{-1}) and the particle concentration (mg l^{-1}) after correcting for particles rejected as pseudofaeces (mg or mg h^{-1} or particles h^{-1}). Three separate ingestion rates were calculated per diet condition: (1) ingestion rate in particles $\text{h}^{-1} \text{ g}^{-1}$; (2) ingestion rate in mg (to calculate whether selection was occurring [Section 2.2.3.1. above] and, (3) ingestion rate in $\text{mg h}^{-1} \text{ g}^{-1}$ (to calculate scope for growth [Section II.5. below]). Ingestion rates in mg h^{-1} were converted to Joules h^{-1} using the values for energy content

determined by wet oxidation of seston filters for each diet (Section 2.2.1.3.).

2.3. Experiment Schedule

Each of the 12 experiments was five days in duration. On day one, the scallops were acclimated on the specific diet for a period of 24 hours. On the second day oxygen consumption rates were determined, while CR was measured on day three. Ammonia excretion rates were measured on day four and biodeposits were processed on day five. Approximately two days later soft tissues were removed from the shell and dry weights determined.

2.4. Estimating Energy Losses

2.4.1. Faeces Production

Directly estimating the absorbed ration (AB) requires a measurement of energy lost in the form of faeces. This requires the complete recovery of all the faeces produced, which can be difficult and impractical. The absorbed ration can be calculated indirectly by determining the absorption efficiency using the Conover (1966), method which does not require the quantitative recovery of faeces. This method was used in my study, simply requires the qualitative recovery of faeces and has the added advantage of simplicity, practicality and low cost over methods such as gravimetric,

radiotracer, indicator and dual-radiotracer techniques (Conover 1966, Widdows 1985).

2.4.1.1. Faeces Processing

Three filters containing faeces from each experimental condition were combusted to determine percent POM, three were processed for wet oxidation and one was used for CN analysis. Four filters per diet condition were combusted to determine absorption efficiency using the Conover (1966) ratio. Each faeces sample was processed in the following manner: samples were thawed and faeces pipetted onto 4.5 cm GF/C pre-ashed, pre-weighed filters and filtered under low vacuum. Faeces filters processed for ash free dry weight were dried at 80° C to constant weight, weighed, combusted at 450° C for 12 hours and then weighed again(\pm 0.01 mg). Faeces filters used for wet oxidation and CN analysis were processed as above.

2.4.1.2. Absorption Efficiency

Absorption efficiency (AE) was estimated according to Conover (1966) using the organic content of the food and the faeces as follows:

$$AE = \frac{(F - E)}{(1 - E) \times F} \times 100$$

where: AE = Absorption efficiency (%)

F = Ash-free dry weight: dry weight ratio in the food

E = Ash-free dry weight: dry weight ratio in the faeces.

To determine the absorption efficiency accurately using this ratio method, the organic matter and ash must be ingested in the same proportions as they occur in the natural food. If pseudofaeces containing a different proportion of POM are produced, selection is taking place and the assumption of the technique is violated. It is then necessary to adjust the estimate of absorption efficiency. If an animal ingests a higher proportion of organic material than inorganic material in their food, the ratio method will underestimate absorption efficiency (Conover 1966). If the percent POM in the ingested ration was different than that in the seston then a corrected AE was calculated by substituting the total percent POM ingested in the Conover ration equation.

2.4.1.3. Absorbed Ration

The absorbed ration or the absorption rate can be calculated from the following equation: $AB = I \times AE$, where AB is the absorption rate in Joules h^{-1} , I is the ingestion rate in Joules h^{-1} and AE is the absorption efficiency

(Thompson and MacDonald 1991). The absorption rate can then be incorporated in the calculation of scope for growth (Section 2.5. below).

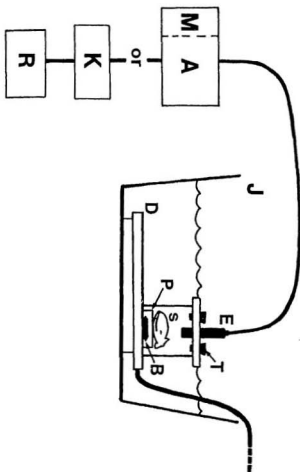
2.4.2. Oxygen Consumption Rate

Scallops were acclimated for 24 hours on a specific diet before measurements of oxygen consumption were made in 300 ml chambers (Figure 2). The centre opening was occupied by a polarographic electrode coupled either to a Radiometer PHM 71 acid base analyzer fitted with a PHA 934 oxygen module or to a Strathkelvin oxygen meter (Model 781b). Signal output was fed to a chart recorder. The scallop was placed on a perforated clear plastic plate overlying a stir bar. Water circulation in the chamber was provided by submersible magnetic stirrers positioned under the perforated plate. The entire chamber and stirring apparatus were immersed in a temperature controlled water bath (J).

Two holes through the chamber cover on either side of the electrode facilitated the filling of the chamber with water and/or displacing excess air. These holes were sealed with rubber stoppers during the experiment. Scallops opened their valves and extended their tentacles immediately after being placed in the chambers filled with fully saturated seawater at 12° C. The decline in partial pressure of

Figure 2. Oxygen Consumption Measurement Apparatus

Legend: A: Radiometer PIM 71 acid base analyzer
B: stir bar
D: submersible stirrer
E: polarographic oxygen electrode
J: temperature controlled water bath
K: Strathkelvin oxygen meter
M: PHA 934 oxygen module
P: perforated plastic plate
R: chart recorder
T: rubber stoppers



oxygen in the chambers was never allowed to drop below 75 % of saturation. Each measurement of oxygen consumption lasted for 50-80 minutes, after which the scallops were returned to the holding tank and fed the appropriate diet overnight until the clearance rate measurements began the following day. All oxygen consumption rates were converted to Joules ($1 \text{ ml O}_2 = 19.9 \text{ J}$) (Winberg 1956).

2.4.3. Ammonia Excretion Rate

Ammonia excretion ($\mu\text{g NH}_4\text{-N}$) was determined by a modified method of Strickland and Parsons (1972) and Widdows (1985) using ammonium sulphate standards (stock solution = 132.1 mg l^{-1}). The seven scallops were removed from the holding tank on day four and each placed in a glass petri dish containing 200 ml of filtered ($0.45 \mu\text{m}$) 12°C seawater. One additional dish containing filtered seawater, but without a scallop, served as the control. Samples were taken (5 ml aliquots) from each dish at 0.5, 1, 2, and 3 hour intervals. Absorbances at 640 nm were recorded for standard solutions and scallop samples using a spectrophotometer. Absorbances for standards were regressed against their corresponding ammonia concentration using the General Linear Model (GLM) procedure of Statistical Analysis

System (SAS Institute Inc 1988) and the equation of the line was determined.

Absorbances for individual scallop samples for each time interval in the diet condition were then converted to ammonium concentration using the regression equation from the standards. A linear regression was then calculated for paired concentrations (μM) and time (h) for each scallop to calculate ammonia concentration during the second hour of the experiment. The second hour of the experiment was chosen because in this time interval the scallop would most likely be in a steady state of ammonia excretion. An individual scallop's ammonia excretion rate ($\mu\text{g NH}_4\text{-N h}^{-1}$) was calculated according to the following equation:

$$\mu\text{g NH}_4\text{-N excreted h}^{-1} = \frac{[A - B] \times 28 \times V}{T}$$

where A = $\text{NH}_4\text{-N}$ in experimental dish (μM)

B = $\text{NH}_4\text{-N}$ in control dish (μM)

V = volume of sea water in dish (l)

T = incubation time (hours)

[1 μM $(\text{NH}_4)_2 \text{SO}_4$ = 28 $\mu\text{g NH}_4\text{-N l}^{-1}$]

All ammonia excretion values were converted to Joules using the conversion factor 1 $\mu\text{g NH}_4\text{-N}$ = 0.025 J (Elliot and Davison 1975).

2.5. Integration of Energy Gain and Losses - Scope for Growth

Scope for growth was first described by Warren and Davis (1967) and is simply the energy available to an animal for gamete and somatic production (growth and reproduction) after maintenance requirements are met. It can be calculated after all the relevant physiological processes (feeding, food absorption, respiration and excretion) have been determined and converted to common energy equivalents (Joules h⁻¹). Scope for growth (SFG) was calculated using the energy balance equation given by Bayne and Newell (1983):

$$SFG = AB - (R + U)$$

where;

AB = absorbed ration, R = energy lost in respiration and U = ammonia excretion.

2.6. Scallop Conditioning Experiment

This series of experiments was conducted to determine whether physiological rates were time dependent or were affected by acclimation to diet mixtures prior to feeding experiments. All the feeding experiments previously described were conducted after scallops were acclimated for 48 hours on the diet mixture. During the four day feeding schedule, clearance rate, ingestion rate, pseudofaeces

production rate and absorption efficiency of the scallops may have changed with respect to time. It was also necessary to determine whether prior feeding at the maintenance ration level affected the response of the scallops to the experimental diet mixtures (i.e. does a scallop's initial condition (supplemented or maintained in sea water) prior to being tested in a physiological experiment effect its performance?). All scallops in the previous studies were fed on natural seston supplemented with approximately one litre of C. muelleri, every one to two days, 2 to 8 weeks prior to being utilized. Fourteen scallops, in the same size range as above, were chosen and separated into two equal groups. One group, designated the supplemented group, was batch fed approximately one litre of C. muelleri and the other, designated the maintained group, was not fed, but received filtered sea water ($< 100 \mu\text{m}$) only. This feeding regime was carried out for approximately two weeks prior to the scallops being used in this experiment. The diet concentration was chosen at 80 % POM at 3 mg l^{-1} because diets of pure algae were relatively easy to prepare and deliver to the scallops, compared to mixed diets. Clearance rate, ingestion rate ($\text{mg h}^{-1} \text{ g}^{-1}$), pseudofaeces production rate ($\text{mg h}^{-1} \text{ g}^{-1}$), faeces organic content (%) and absorption efficiency (uncorrected and corrected for selection) were

calculated each day for each scallop. Two faeces samples per group (maintained or supplemented) per time period were taken for determination of percent organic content. All procedures, including collection and processing of biodeposits, were conducted as described above (see estimating energy uptake and energy losses). There were no significant differences in shell height (Student's $t = -0.4711$, $df = 12$, $P = 0.6460$) or dry tissue weight (Student's $t = 1.2622$, $df = 12$, $P = 0.2308$) between the maintained and supplemented groups. Physiological rates were converted to a standard scallop (1 g tissue weight) as for the physiological experiments.

2.7. Statistical Analysis

All statistical procedures were carried out using the General Linear Model (GLM) procedure of the Statistical Analysis System (SAS Institute Inc. release 6.03 edition). A one way analysis of variance (ANOVA) was used to determine if mean diet concentrations were different for the four different diet groups (Section 2.1.2.). The null hypothesis tested was that concentrations measured for each group are random samples from populations having the same mean value (i.e. $\mu_1 = \mu_2 = \mu_3 = \mu_4$). A one way ANOVA was also conducted

on mean percent POM for the three different levels of diet quality (i.e. 25, 50, and 80% POM).

A one way ANOVA was conducted on the scallop shell height and scallop dry tissue weight data to determine if there was any significant difference between the means of the 12 diet groups. The null hypothesis tested was that the 12 scores in each group are random samples from populations having the same mean value where $\mu_1 = \mu_2 = \mu_3 \dots = \mu_{12}$.

Two way ANOVAs were conducted using the following physiological rates as dependent variables: active and routine clearance rates; pseudofaeces production rate; respiration rate; ammonia excretion rate and faeces POM. The independent variable was diet condition. The null hypothesis tested was that each physiological rate was independent of diet (i.e. the 12 sets of scores were random samples from populations where $\mu_1 = \mu_2 = \mu_3 = \dots = \mu_{12}$). A one way ANOVA was conducted on absorption efficiency (uncorrected and corrected for selection through the production of pseudofaeces) as the dependent variable and seston concentration as the independent variable. This is because estimates of absorption efficiency were derived from the quality of the faeces and diet. Two way ANOVAs could not be conducted on ingestion rate or on scope for growth because both physiological rates are a function of seston

concentration and seston POM (i.e. a comparison of ingestion rate versus concentration is equal to regressing x/y versus y ; ingestion rate will inevitably show some relationship). As a result, only the trends (without statistical analysis) for ingestion rate and scope for growth versus seston concentration and POM were discussed.

For all comparisons a significance level of $\alpha = 0.05$ was used. If significant F values were achieved in any ANOVA, a GLM Student Newman-Keuls test was conducted to determine which means were significantly different from one another. Prior to statistical analyses, data were tested for normality and homogeneity of variance using a Shapiro-Wilk W. test (Zar 1984) and an F-max test (Sokal and Rohlf 1981) respectively. If the data violated one of the above ANOVA requirements the data was transformed to Log_{10} according to Zar (1984) and the ANOVA was conducted again. If the data still violated one of the assumptions, a non-parametric Kruskal-Wallis single factor ANOVA by ranks test (Zar 1984) was employed for one way ANOVA data sets and a non-parametric two-factor ANOVA, which is an extension of the single factor Kruskal-Wallis test (Zar 1984), was employed for the two way ANOVA data sets.

Data obtained in the scallop conditioning experiment were evaluated using analysis of variance with repeated

measures test (ANOVAR). Physiological rates of the scallops were used as the dependent variables, and time (hours) and group (starved or maintained) as the two independent variables. The SAS GLM procedure simultaneously conducts both a univariate (ANOVAR) and a multivariate analysis (MANOVAR). Potvin et al. (1990) outline the selection criteria for choosing an ANOVAR or MANOVAR test. Prior to examination of the ANOVAR results, the hypothesis of sphericity was tested (Mauchly's criterion). If the assumption of sphericity was not violated, a univariate procedure was used (ANOVAR); if this assumption was violated, then the H-F ϵ (epsilon) indication of homogeneity of variance was examined. If the H-F $\epsilon \approx 1$, and the Huynh-Feldt (H-F) and Greenhouse-Geisser (G-G) significance levels agreed, a univariate procedure was still used. If this was not the case, then a multivariate procedure was used (MANOVAR).

3. Results

3.1. Experimental Conditions

3.1.1. General Measurements

Mean shell heights and tissue weights (\pm s.d.) for scallops in each experiment are reported in Table 1. The following coding system for experimental diet mixture will be used throughout the text. The last 2 digits represent the percent POM and the first 1 to 2 digits represent the concentration in mg (i.e. 3-25 is 3 mg l⁻¹ and 25 % POM while 14-80 represents a concentration of 14 mg l⁻¹ and 80 % POM). Mean shell height ranged from 47.1 ± 4.1 mm in the 3-25 diet to 55.0 ± 1.8 mm in the 14-80. Mean dry tissue weight ranged from 0.41 ± 0.13 g in the 3-25 diet to 1.14 ± 0.29 g in the 14-25 diet (Table 1).

One way ANOVA was performed on shell height and dry tissue weight to see if there was any significant difference in the size of the scallops between each diet treatment (independent variable). The normality and homogeneity of variance assumptions were violated in the untransformed and log₁₀ transformed data for both shell height and dry tissue weight, so a nonparametric Kruskal-Wallis single factor ANOVA by ranks test was carried out. There was a significant difference between the mean shell heights (Chi-Square =

Table 1. Mean shell height (ht.) mm and mean dry tissue weight (wt.) g and Student Newman-Keuls test grouping for scallops for each experimental diet.*

Experimental diet mixture mean shell ht. and SNK grouping \pm s.d. *			Experimental diet mixture, mean dry tissue wt. and SNK grouping \pm s.d. *		
14-80	A	55.0 \pm 2.1	1-25	A	1.22 \pm 0.32
14-50	A B	53.0 \pm 1.9	14-80	A	1.20 \pm 0.29
7-80	A B	51.4 \pm 3.0	14-25	A B	1.14 \pm 0.29
14-25	A B C	51.3 \pm 2.7	14-50	A B C	0.97 \pm 0.32
1-25	B C	50.7 \pm 2.1	7-80	A B C	0.95 \pm 0.23
3-50	C D	49.5 \pm 3.1	1-80	A B C	0.94 \pm 0.38
1-80	C D	49.6 \pm 1.3	7-25	A B C	0.84 \pm 0.23
7-25	C D	49.7 \pm 2.1	1-50	B C	0.76 \pm 0.12
1-50	C D	49.6 \pm 0.6	3-50	C D	0.65 \pm 0.16
3-80	C D	49.2 \pm 0.6	7-50	D E	0.61 \pm 0.03
7-50	C D	47.1 \pm 4.1	3-25	E	0.57 \pm 0.10
3-25	D	47.7 \pm 1.9		E	0.41 \pm 0.13

* Experimental diet mixtures are ranked based on mean shell ht. or mean dry tissue wt. from highest to lowest in descending order. Diets with the same letter are not significantly different.
N.B. SNK = Student Newman-Keuls

39.108, $P < 0.001$ and $F = 5.83$, $P < 0.001$) and mean dry tissue weights among diets (Chi-Square = 55.316, $P < 0.001$ and $F = 13.08$, $P < 0.001$). The Student Newman-Keuls test showed a significant difference among the mean sum of the ranked shell heights and dry tissue weights as shown in Table 1. Attempts were made throughout to use the same size scallops (ca. 50 mm) but seasonal availability and great variations in body tissue weights made this difficult. For example, the scallops in the 1-25 diet (1.22 g) were approximately 3 times heavier than counterparts in the 3-25 diet (0.41 g) but were only about or 3.6 mm greater in shell height. This emphasizes the need to standardize, by weight alone, the various physiological rates to a standard size scallop (1.0 g) for direct comparisons between different diet treatments.

3.1.2. Experimental Diet Mixtures

Particle concentrations and percent POM of experimental diets were determined on the same day as the clearance rates were measured. Values for particle concentration and percent POM during each experiment are provided in Table 2. Experimental diet mixtures were chosen to give a range of both concentration and percent organic content (i.e. 1, 3, 7 and 14 mg l⁻¹, 25%, 50% and 80% POM). Table 2 shows that

Table 2. Theoretical and obtained experimental diet mixtures [concentrations (mg l⁻¹) and percent POM (%)] and obtained particle counts (part. ml⁻¹)

Theoretical experimental diet mixture (mg l ⁻¹ POM)	Actual obtained diet concentration (mg l ⁻¹) s.d. \pm	Actual obtained diet POM (%) s.d. \pm	Actual obtained particle count (part. ml ⁻¹) s.d. \pm
1-25	1.22 \pm 0.83	29.7 \pm 3.6	8,252 \pm 444
3-25	2.67 \pm 0.56	23.0 \pm 0.8	22,160 \pm 122
7-25	7.46 \pm 1.06	23.0 \pm 2.4	39,941 \pm 3,428
14-25	15.43 \pm 5.89	29.3 \pm 5.7	71,720 \pm 5,780
1-50	0.85 \pm 0.35	46.0 \pm 6.7	10,145 \pm 296
3-50	2.35 \pm 1.60	45.9 \pm 1.6	31,105 \pm 3,420
7-50	9.07 \pm 2.61	48.2 \pm 3.0	65,300 \pm 4,740
14-50	14.24 \pm 4.21	45.5 \pm 11.1	111,340 \pm 3,360
1-80	0.69 \pm 0.11	87.0 \pm 0.11	17,834 \pm 316
3-80	2.59 \pm 0.98	82.1 \pm 16.5	42,170 \pm 2,836
7-80	5.15 \pm 0.91	68.0 \pm 7.2	97,420 \pm 2,100
14-80	13.55 \pm 1.68	80.6 \pm 0.1	161,380 \pm 5,000

N.B. a silica particle weighed $\approx 4.4 \times$ greater than a C. muelleri cell (Appendix A)

there is a slight difference between the theoretical and obtained values. As a result of these small discrepancies, a nonparametric Kruskal-Wallis single factor ANOVA by ranks was used to test for difference between concentration and the four diet groups (because assumptions of normality and homogeneity of variance of both untransformed and transformed data were violated). There were significant differences in concentrations among all four experimental groups ($F = 438.48$, $df = 3$, $P < 0.001$) determined with a Student Newman-Keuls (SNK) test (Table 3). A one way ANOVA and SNK test revealed a significant difference between all three levels of POM selected for the experimental diets ($F = 239.85$, $df = 3$, $P < 0.001$) (Table 3). To be consistent with the results obtained using a non-parametric test for concentration, a non-parametric Kruskal-Wallis single factor ANOVA was also used to analyze percent POM for the three groups. This test confirmed the significant difference ($F = 242.78$, $df = 3$, $P < 0.001$) among the means of the three experimental organic levels but the results were not included in Table 3.

Table 3. Student Newman-Keuls test for measured mean diet concentration (mg l^{-1}) and measured mean diet percent POM (%).

SNK grouping for measured mean diet concentration (non parametric ANOVA) *	SNK grouping for measured mean diet percent POM (parametric ANOVA) *
14 A	80 A
7 B	50 B
3 C	25 C
1 D	

* Experimental diet mixtures are ranked on mean concentration or mean percent POM from highest to lowest in descending order. Diets with the same letter are not significantly different.

N.B. SNK = Student Newman-Keuls

3.2. Estimating Energy Uptake

3.2.1. Clearance Rate

3.2.1.1. Energy Content of Diets

The energy content of the diet mixtures (Joules mg^{-1}), determined from wet oxidation, is the mean of three water samples collected at the beginning, middle and end of the clearance rate experiment (Table 4). The energy content of the seston should not have changed significantly as concentration increased for a particular level of POM. However, there was some unexplained variation in the seston quality (i.e. 25 % organic diet). Some of the variation may have been due to fluctuations in the quality of algae from one batch to another or errors associated with titration techniques. The overall mean energy content of the seston increased with increasing percent POM. The overall mean (column 3, Table 4) for each of the three levels of POM was used to calculate ingestion rate and the absorption in Joules h^{-1} . The CN quality results of seston were extremely variable (see Appendix Table D.1.). The particulate organic carbon (POC) or particulate organic nitrogen (PON) content of the seston should not have changed significantly as concentration increased for a particular level of POM. The Perkin Elmer CHN analyzer cannot accurately analyze seston samples containing more than 10 mg l^{-1} on a single filter.

Table 4. Energy content of seston (experimental diet mixtures) derived by wet oxidation.

Experimental diet mixture (mg l ⁻¹ POM)	Mean energy of seston (Joules mg ⁻¹) ± s.d.	Grand mean energy of seston * (Joules mg ⁻¹) ± s.d.
1-25	5.68 ± 1.29	4.14 ± 1.47
3-25	4.01 ± 0.90	
7-25	2.74 ± 0.27	
14-25	N/A **	
1-50	5.59 ± 2.10	4.72 ± 1.12
3-50	5.44 ± 0.85	
7-50	4.72 ± 1.72	
14-50	3.14 ± 0.13	
1-80	10.62 ± 1.86	9.21 ± 1.80
3-80	10.87 ± 1.08	
7-80	7.32 ± 2.82	
14-80	8.03 ± 0.00	

* The Grand Mean is the mean of all four mean values for energy of seston per organic level.

Accordingly, variation in samples may have resulted from having to cut each of the filters into 2 or more pieces to be processed, thus losing some of the seston in the process. Regardless, CN analysis of the seston samples was not used to calculate energy balance of the scallops in this study and was conducted only as an additional indicator of seston quality.

3.2.1.2. Clearance Rate

Active clearance rates (\pm s.d. 1 h^{-1}) versus concentration (mg l^{-1}) and percent POM are shown in Figure 3A and 3B respectively. Routine clearance rates (not shown) are typically 5-25 % lower than active clearance rates. After standardizing active clearance rate to scallops of 1 g body weight, the corrected values ($1 \text{ h}^{-1} \text{ g}^{-1}$) were tested with percent POM and concentration as the independent variables (two way ANOVA). The raw data violated the homogeneity of variance assumption and was therefore \log_{10} transformed. The test results indicated a significant concentration effect ($F = 39.20$, $df = 3$, $P < 0.001$), a significant effect due to percent POM ($F = 11.98$, $df = 2$, $P < 0.001$) and an interaction effect ($F = 2.23$, $df = 6$, $P = 0.050$). There was a significant difference among the mean active clearance rates at the four different concentrations (Table 5). Data

Figure 3. A) Active clearance rate ($l\ h^{-1}\ g^{-1}$) versus seston concentration ($mg\ l^{-1}$). B) Active clearance rate ($l\ h^{-1}\ g^{-1}$) versus seston POM (%).

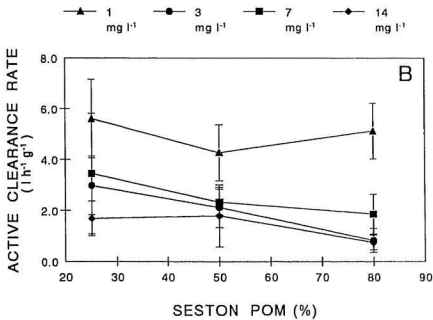
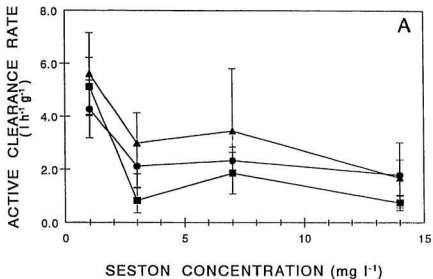


Table 5. Student Newman-Keuls test grouping for mean active and mean routine clearance rates.

SNK grouping for mean active clearance rate by conc. *	SNK grouping for mean active clearance rate by POM *	SNK grouping for mean routine clearance rate by conc. *	SNK grouping for mean routine clearance rate by POM *
1 A	25 A	1 A	25 A
7 B	50 B	7 B	50 B
3 B C	80 B	3 B C	80 B
14 C		14 C	

* Mean active and routine clearance rates are ranked by diet concentration (conc.) and percent POM from highest to lowest in descending order. Clearance rates with same letter are not significantly different.

N.B. SNK = Student Newman-Keuls

for the 1 mg l⁻¹ diets were significantly higher than those for the 3, 7 and 14 mg l⁻¹ diets. The same results were observed for the standardized routine clearance rates (Table 5). The trend, therefore, is that active clearance rate decreases with increasing seston concentration between 1 and 3 mg l⁻¹, and then plateaus (increasing only slightly at a seston concentration of 7 mg l⁻¹) between 3 and 14 mg l⁻¹ (Figure 3A).

The SNK revealed no significant difference in clearance rate (CR) between the 50 and 80 % organic levels but values for these two levels were both significantly lower than rates recorded for the 25 % organic level (Table 5). The same results were observed for the standardized routine CRs (Table 5). Clearance rate, therefore decreased with increasing seston POM between 25 and 50 % POM and then became independent of seston quality between 50 and 80 % POM (Table 5). The highest mean active CRs were observed at the poorest quality diet (25 % POM level) while the lowest rates occurred at the best quality diet (80 % organic level) (Figure 3B). The interaction effect means that the effect of concentration was not independent of the presence of a particular level of POM. The slight interaction can be seen in Figure 3B particularly between 1 and 3 mg l⁻¹ and between 7 and 14 mg l⁻¹.

3.2.2. Pseudofaeces

When calculating pseudofaeces production rates, the control samples collected (equivalent volumes of diet mixtures collected during the experiment representing background levels for seawater) had higher weights (mg) but lower concentrations (particles hr^{-1}) than recorded in scallop samples. Contamination of the controls and weighing errors were thought to be the problem. Therefore, a control or sea water blank for each diet was calculated using the mean part. ml^{-1} and the mean weight (mg l^{-1}) determined from the dry weight of diet and particle count for each diet (Section 2.2.1.2. above). For example, scallop # 1 fed a 1-25 diet produced pseudofaeces which was diluted with 20 ml of sea water for a total count of 3.254×10^6 particles. All pseudofaeces samples were suspended in 20 ml of sea water for ease in counting with the Coulter Multisizer. The mean concentration for this diet mixture was 8×10^3 part. ml^{-1} . The mean sea water background blank to be subtracted from the pseudofaeces sample therefore was 1.60×10^5 particles (i.e. $20 \text{ ml} \times 8 \times 10^3$ part. ml^{-1}). This gave a pseudofaeces amount of 3.09×10^6 particles for this scallop over the duration of the CR experiment. This procedure was used for each scallop in each diet and the amount of pseudofaeces produced was expressed in particles h^{-1} . In addition, the

weight of the pseudofaeces sample for each scallop was also determined and a mean sea water background blank was subtracted giving a individual pseudofaeces amount in mg. All pseudofaeces amounts (expressed in mg h^{-1} or in particles h^{-1}) were standardized for a 1 g scallop.

Mean pseudofaeces production rates (part. $h^{-1} g^{-1}$) for each diet are shown in Table 6 and in Figures 4A and 4B. The mean pseudofaeces rate ranged from 0.05×10^6 to 2.74×10^6 (part. $h^{-1} g^{-1}$) (Table 6). The greatest amount of pseudofaeces produced was observed at the highest seston concentration and organic mixture (i.e. 14-80 diet). It is interesting that pseudofaeces were also produced at the lower level diets (i.e. 1-25 and 1-50 diets).

Total particles cleared and rejected for active and routine CRs at all diet levels are reported in Table 6. The mean percent of the material cleared and then rejected as pseudofaeces (based on part. $h^{-1} g^{-1}$) ranged from 0.1 (0.1 s.d.) to 3.5 (2.2 s.d.) percent for active CRs and 0.1 (0.1 s.d.) to 7.2 (6.9 s.d.) for routine CRs (Table 6). The 3-80 diet showed the highest mean percent material rejected as pseudofaeces partially due to low CRs (Table 6).

Both the untransformed and the transformed pseudofaeces data for the two way ANOVA violated the normality and homogeneity of variance assumptions, so a non

Figure 4. A) Pseudofaeces Production rate ($\text{part. h}^{-1} \text{g}^{-1}$)
versus seston concentration (mg l^{-1}). **B)**
Pseudofaeces production rate ($\text{part. h}^{-1} \text{g}^{-1}$)
versus seston POM (%).

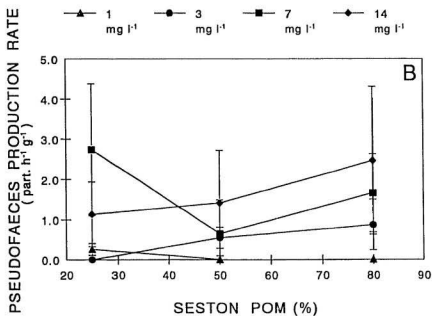
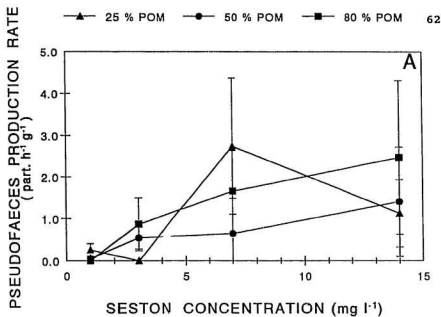


Table 6. Mean pseudofaeces production rate, mean active and routine total particles cleared and mean active and routine percent material rejected.

Experimental diet mixture (mg l ⁻¹ POM) and N**	Mean pseudofaeces rate (part. h ⁻¹ g ⁻¹ x 10 ³) ± s.d.	Mean active total particles cleared (part. h ⁻¹ g ⁻¹ x 10 ³) ± s.d.	Mean routine total particles cleared (part. h ⁻¹ g ⁻¹ x 10 ³) ± s.d.	Mean active percent material rejected (%) ± s.d.	Mean routine percent material rejected (%) ± s.d.
1-25 7,7	2.6 ± 1.5	4.7 ± 1.3	4.4 ± 1.5	0.6 ± 0.4	0.6 ± 0.4
3-25 0,7	N/A *	6.1 ± 2.5	6.2 ± 2.7	N/A *	N/A *
7-25 7,7	27.4 ± 16.4	13.8 ± 9.5	12.8 ± 8.1	2.5 ± 1.3	2.8 ± 1.8
14-25 7,7	1.3 ± 8.1	12.1 ± 4.9	10.7 ± 4.5	1.1 ± 0.8	1.2 ± 0.8
1-50 2,7	0.5 ± 0.6	4.3 ± 1.1	3.8 ± 1.1	0.1 ± 0.1	0.1 ± 0.1
3-50 7,7	5.4 ± 2.6	6.6 ± 2.5	5.7 ± 3.1	1.0 ± 0.5	1.7 ± 2.2
7-50 7,7	6.5 ± 8.4	15.2 ± 3.4	11.7 ± 4.2	0.5 ± 0.6	0.6 ± 0.8
14-50 7,7	14.1 ± 13.1	19.9 ± 13.7	16.8 ± 9.6	0.7 ± 0.3	0.8 ± 0.5
1-80 0,7	N/A *	9.1 ± 2.0	7.6 ± 2.2	N/A *	N/A *
3-80 6,6	8.7 ± 6.3	3.5 ± 2.0	2.1 ± 1.5	3.5 ± 2.2	7.2 ± 6.9
7-80 7,7	16.7 ± 9.8	18.1 ± 7.6	13.6 ± 8.7	1.0 ± 0.6	2.4 ± 3.2
14-80 7,7	24.7 ± 18.4	12.2 ± 4.7	10.3 ± 6.3	1.9 ± 1.1	2.5 ± 1.1

* No pseudofaeces produced

** Number of scallops for Mean pseudofaeces rate (part. h⁻¹ g⁻¹) followed by number of scallops for the remaining variables (ie. mean active and routine total particles cleared (part. h⁻¹ g⁻¹) and percent material rejected (%)).

-parametric two factor Kruskal-Wallis test was employed. The results of the ANOVA indicated a significant concentration effect ($F = 8.96$, $df = 3$, $P < 0.001$), a significant organic level effect ($F = 4.89$, $df = 2$, $P < 0.05$) and a significant interaction ($F = 2.94$, $df = 4$, $P < 0.05$). The SNK test showed that the mean pseudofaeces production rates (part. $h^{-1} g^{-1}$) for the 14 and 7 $mg\ l^{-1}$ diets were not significantly different from one another but were both significantly higher than the mean pseudofaeces rates for the 3 $mg\ l^{-1}$ diets which in turn was greater than rates for the 1 $mg\ l^{-1}$ diet (Table 7). The trend was pseudofaeces production rate increased with particle concentration up to 7 $mg\ l^{-1}$.

The SNK test showed no significant difference between mean pseudofaeces rates (part. $h^{-1} g^{-1}$) for the 25 and the 80 % organic levels (Table 7) plus the rates for the 25 % level were not statistically greater than those observed at 50 % organic level (Table 7). This suggests the scallop's mean pseudofaeces production rate decreased between 25 and 50% POM and then increased again between 50 and 80% POM. The interaction effect indicates that the effect of concentration on pseudofaeces rate was not independent of the presence of a organic content. This interaction can be seen clearly in both Figure 4A and 4B.

Table 7. Student Newman-Keuls test grouping for mean pseudofaeces production rate (part. h⁻¹ g⁻¹)

SNK grouping for mean pseudofaeces rate by concentration *	SNK grouping for mean pseudofaeces rate by POM *
14 A	80 A
A	A
7 A	25 A B
3 B	B
50 B	B
1 C	

* Mean pseudofaeces production rates are ranked by diet concentration and percent POM from highest to lowest in descending order. Diets with the same letter are not significantly different.

N.B. SNK = Student Newman-Keuls

3.2.2.1. Selection Process

The percentages of POM in all pseudofaeces samples were compared to levels of POM in the respective diets to determine whether scallops were preferentially rejecting inorganic particles. Selection had occurred if there was significantly less organic material in the pseudofaeces than the diet. Mean percent POM for the 12 diets, mean total percent POM ingested (%) (after corrections for the amount (mg) and percent POM (%) in pseudofaeces) and the mean percent enhancement are shown in Table 8. Percent POM in the 25 %, 50 % and 80 % diets at the four concentrations are compared to the respective ingested rations in Figures 5, 6 and 7 respectively. Also the percent enhancement (percentage of diet enhanced above or below the percent POM of the diet) plus standard deviations are presented in Figures 5, 6 and 7.

All percent enhancement values were tested for significance against zero with a parametric Student T-test. If the data violated the normality assumption (Shapiro-Wilk W. test, Zar 1984) a non-parametric Wilcoxon signed-ranks test was employed. Scallops altered the mean total percent organic content ingested in eight out of the ten diets in which pseudofaeces were produced (Table 8). A significant negative enhancement of -6.0 with a range of ± 2.0 % was observed for scallops exposed to the 14-25 diet (Table 8 and

Table 8. Mean diet percent POM, mean total percent POM ingested, mean percent enhancement and Student T-test for percent enhancement.

Experimental diet mixture (mg l ⁻¹ POM)	Mean diet percent POM \pm s.d.	Mean total percent POM \pm s.d.	Mean percent enhancement \pm s.d.	T-test type for percent enhancement	Significant from zero
1-25	29.7 \pm 3.6	29.6 \pm 0.2	-0.4 * 0.6	P	NS
3-25	23.0 \pm 0.8	23.0 \pm 0.8	N/A **	N/A **	N/A **
7-25	23.0 \pm 2.4	22.3 \pm 0.4	-3.4 * 2.0	P	NS
14-25	29.3 \pm 5.7	27.5 \pm 1.2	-6.0 * 3.8	P	S
1-50	46.0 \pm 6.7	45.9 \pm 0.2	-0.4 * 0.6	P	NS
3-50	45.9 \pm 1.6	46.8 \pm 2.2	+2.0 * 4.7	P	NS
7-50	48.2 \pm 3.0	50.5 \pm 1.6	+8.9 * 11.1	NP	S
14-50	45.5 \pm 11.1	45.8 \pm 0.2	+6.5 * 4.5	NP	S
1-80	87.0 \pm 0.1	87.0 \pm 0.1	N/A **	N/A **	N/A **
3-80	82.1 \pm 16.5	93.6 \pm 6.9	+13.9 * 8.5	P	S
7-80	68.0 \pm 7.2	71.4 \pm 2.1	+5.0 * 3.1	P	S
14-80	80.6 \pm 0.1	90.8 \pm 6.4	+11.8 * 8.4	NP	S

* The range is given instead of the standard deviation due to the fact the values indicate values above or below zero percent enhancement.

** N/A means not available.

N.B. P is a parametric Student's test, NP is a non parametric Wilcoxon signed-ranks test, S means the percent enhancement value is significantly different from zero and NS means the former is not significantly different from zero.

Figure 5. Seston POM (%), percent POM ingested by scallops (%) and percent enhancement (%) of scallops fed the 25 % POM diet versus seston concentration (mg l^{-1}). Asterisk indicates significant percent enhancement.

25 % POM DIET

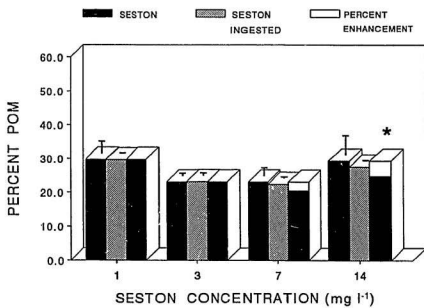


Figure 6. Seston POM (%), percent POM ingested by scallops (%) and percent enhancement (%) of scallops fed the 50 % POM diet versus seston concentration (mg l^{-1}). Asterisk indicates significant percent enhancement.

50 % POM DIET

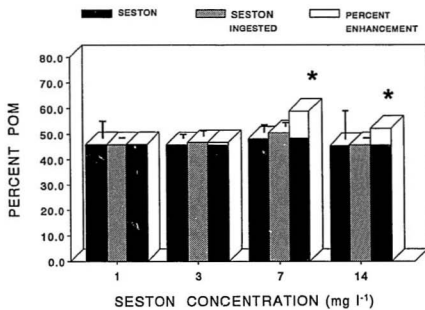


Figure 7. Seston POM (%), percent POM ingested by scallops (%) and percent enhancement (%) of scallops fed the 80 % POM diet versus seston concentration (mg l⁻¹). Asterisk indicates significant percent enhancement.

80 % POM DIET

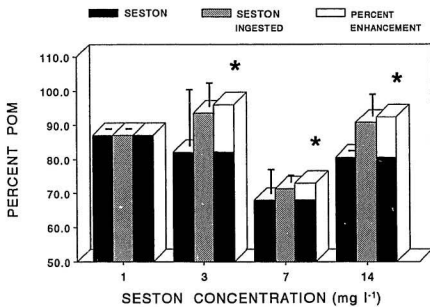


Figure 5). Significant positive enhancement was recorded for animals from all the 80 % diets where pseudofaeces were produced and the two highest concentrations (7 and 14) in the 50 % diets (Table 8, Figures 5 and 6). When there was significant enhancement, positive or negative, it was necessary to make the appropriate correction to the ingested ration before calculating absorption efficiency (i.e. the seston POM ingested is no longer the same as the seston POM fed to scallops) (see Section 3.4.1.2 below). For comparative purposes two absorption efficiencies were calculated for each diet mixture, one using the mean percent POM initially fed to the scallops (i.e. assumes no selection) and the second using the mean total percent POM ingested after correction for selection.

Mean pseudofaeces production rates ($\text{mg h}^{-1} \text{g}^{-1}$) and the amount of material rejected, expressed as a percent of the material cleared using active and routine CRs, are shown in Table 9. Statistical analysis was not performed on the mean pseudofaeces production rates (mg h^{-1}) because these values were predicted from a regression equation of pseudofaeces production versus seston concentration (equation: Pseudo. amount (mg) = $0.9916 \times \text{Concentration (mg l}^{-1}) - 1.0339$; see Section 2.2.3.1 above). The same trends were observed for pseudofaeces production in mg as observed for the number of

Table 9. Mean pseudofaeces production rate ($\text{mg h}^{-1} \text{g}^{-1}$), mean active and routine percent material rejected by weight.

Experimental diet mixture (mg l^{-1} POM)	Mean pseudofaeces production rate ($\text{mg h}^{-1} \text{g}^{-1}$) \pm s.d.	Mean active percent rejected by weight (%) \pm s.d.	Mean routine percent rejected by weight (%) \pm s.d.
1-25	0.17 ± 0.7	2.54 ± 1.08	2.66 ± 1.10
3-25	N/A *	N/A *	N/A *
7-25	0.98 ± 3.4	5.04 ± 2.51	5.50 ± 3.32
14-25	2.08 ± 0.37	9.77 ± 5.34	11.31 ± 6.43
1-50	$0.09 \pm **$	$1.82 \pm **$	$2.22 \pm **$
3-50	0.30 ± 0.09	6.43 ± 2.34	10.29 ± 10.37
7-50	1.82 ± 0.22	8.83 ± 1.34	13.18 ± 7.31
14-50	2.13 ± 0.40	11.66 ± 6.44	12.79 ± 6.67
1-80	N/A *	N/A *	N/A *
3-80	0.28 ± 0.13	20.01 ± 20.37	31.62 ± 19.95
7-80	0.62 ± 0.12	8.15 ± 5.49	9.46 ± 5.19
14-80	1.52 ± 0.31	15.78 ± 4.14	26.09 ± 21.49

* No pseudofaeces produced.

** Only two out of seven scallops produced small amount of pseudofaeces for this diet. Therefore two pseudofaeces samples were pooled onto one filter.

particles produced (Figure 4A, B). The mean percent material cleared and then rejected (by weight) using routine and active CRs was highest at the 3-80 and 14-80 diets respectively (Table 9).

3.2.3. Ingestion Rate

There were three separate ingestion rates calculated per diet mixture; in particles $\text{h}^{-1} \text{g}^{-1}$; in mg (corrected for selection) (Section 2.2.3.1. above) and in $\text{mg h}^{-1} \text{g}^{-1}$ for the determination of scope for growth (Section 2.5. above).

Mean active ingestion rates ($\text{part. h}^{-1} \text{g}^{-1}$) versus concentration (mg l^{-1}) and seston POM are shown in Figures 8A and 8B, respectively. The lowest mean active ingestion rate was found with the 3-80 diet, at $34.5 \pm 19.7 \times 10^6 \text{ part. h}^{-1} \text{g}^{-1}$ and the highest mean rate was found with the 14-50 diet at $197.6 \pm 135.1 \times 10^6 \text{ part. h}^{-1} \text{g}^{-1}$ (Table 10).

Ingestion rate increased with increasing seston concentration between 1 and 7 mg l^{-1} and then appeared to plateau between 7 and 14 mg l^{-1} (Figure 8A). This trend resulted from a significant levelling off in clearance rate and pseudofaeces production with increasing seston concentration. Ingestion rate does not appear to change with increasing seston POM (Figure 8B). This is due to a significant decrease then plateau in clearance rate plus a

Figure 8. A) Active ingestion rate (part. $\text{h}^{-1} \text{g}^{-1}$) versus seston concentration (mg l^{-1}). **B)** Active ingestion rate (part. $\text{h}^{-1} \text{g}^{-1}$) versus seston POM (%).

—▲— 25 % POM —●— 50 % POM —■— 80 % POM 78

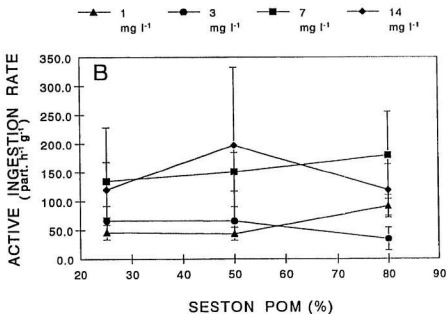
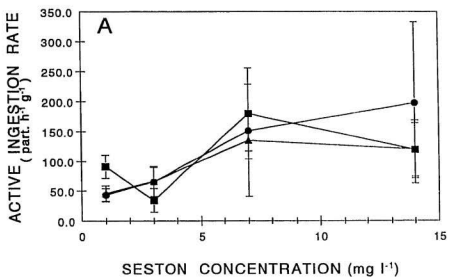


Table 10. Mean active and mean routine ingestion rate (part. h⁻¹ g⁻¹).

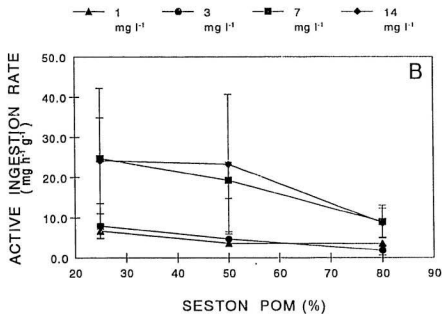
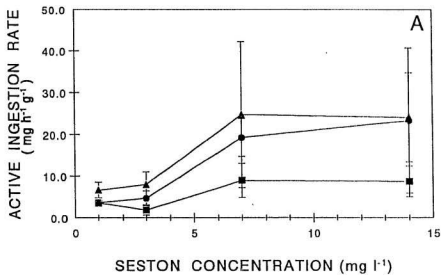
Experimental diet mixture (mg l ⁻¹ POM)	N	Mean active ingestion rate (part. h ⁻¹ g ⁻¹ x 10 ⁷) ± s.d.	Mean routine ingestion rate (part. h ⁻¹ g ⁻¹ x 10 ⁷) ± s.d.
1-25	7	4.6 ± 1.3	4.3 ± 1.5
3-25	6	6.6 ± 2.5	6.3 ± 2.7
7-25	7	13.5 ± 9.4	12.6 ± 8.1
14-25	7	12.0 ± 4.8	10.6 ± 4.5
1-50	7	4.3 ± 1.1	3.9 ± 1.1
3-50	7	6.5 ± 2.5	5.6 ± 3.1
7-50	7	15.1 ± 3.3	11.6 ± 4.2
14-50	7	19.8 ± 13.5	16.7 ± 9.5
1-80	7	9.1 ± 2.0	7.6 ± 2.2
3-80	6	3.4 ± 1.9	2.0 ± 1.5
7-80	7	18.0 ± 7.6	13.4 ± 8.7
14-80	7	11.9 ± 4.5	10.1 ± 6.1

significant oscillation in pseudofaeces production rate versus seston POM.

Ingestion rates (mg) were also calculated to determine if the scallop could alter the quality of the diet to be ingested. Only the routine CR values (i.e. zero values included) were used in these calculations. If the scallops were not feeding they could not be producing pseudofaeces and preferentially selecting organic particles as discussed in Section 2.2.3.1. Routine clearance rates and ingestion rates were not corrected to a 1 g scallop tissue weight because the objective was to determine a scallop's total percent POM ingested during the CR experiment (Table 8). These values were then compared to the diet percent POM to determine whether enhancement had occurred (Section 3.2.3.1).

Ingestion rate was also calculated in $\text{mg h}^{-1} \text{g}^{-1}$ to derive scope for growth. Mean active ingestion rates ($\text{mg h}^{-1} \text{g}^{-1}$) versus seston concentration (mg l^{-1}) and seston POM are shown in Figures 9A and 9B respectively. The lowest mean rate was found with the 3-80 diet at 1.86 ± 1.21 ($\text{mg h}^{-1} \text{g}^{-1}$) and the highest mean active ingestion rate was observed for the 7-25 diet at 24.74 ± 17.48 ($\text{mg h}^{-1} \text{g}^{-1}$). The trend appears to be that mean ingestion rate ($\text{mg h}^{-1} \text{g}^{-1}$) is independent of concentration between 1 and 3 mg l^{-1} (except

Figure 9. A) Active ingestion rate ($\text{mg h}^{-1} \text{g}^{-1}$) versus seston concentration (mg l^{-1}). B) Active ingestion rate ($\text{mg h}^{-1} \text{g}^{-1}$) versus seston POM (%).



for the 3-80 diet); increases with increasing concentration between 3 and 7 mg l⁻¹ and then appears to become independent of concentration again between 7 and 14 mg l⁻¹ (Figure 9A). This trend is due to a significant decrease then plateau in clearance rate along with a significant increase then plateau in pseudofaeces production rate with increasing seston concentration. Ingestion rate appears to decrease with increasing seston POM (Figure 9B). This explained by a significant plateau in clearance rate between the 50 and 80 % seston POM diets plus the fact the highest amount of pseudofaeces was produced at the 80 % POM diets.

3.3. Estimating Energy Losses

3.3.1. Faeces Production

3.3.1.1. Faeces

The only analysis performed on samples of faecal material was weight loss on ignition to determine the ash free dry weight and organic percentage. Some samples were processed for wet oxidation analysis, but due to technical difficulties in determining the titration end point many data were unusable. The mean percent POM of scallop faeces for each diet mixture ranged from a maximum of 24.4 ± 7.9 for scallops exposed to the 7-80 diet to of 17.3 ± 0.7 observed for the 1-25 diet (Table 11). The mean faeces

Table 11. Mean percent organic content of faeces (%), mean absorption efficiency (AE; %) and mean absorption efficiency corrected for selection (AEC; %).

Experimental diet mixture (mg l ⁻¹ POM)	N	Faeces organic content (%) \pm s.d.	AE (%) \pm s.d.	AEC (%) \pm s.d.
1-25	3	17.3 \pm 0.7	50.6 \pm 2.5	50.6 \pm 2.1
3-25	3	17.5 \pm 1.2	29.2 \pm 5.9	29.2 \pm 5.9
7-25	3	19.2 \pm 0.9	21.5 \pm 4.3	16.6 \pm 1.7
14-25	2	19.0 \pm 0.1	43.4 \pm 0.5	40.9 \pm 0.4
1-50	3	24.3 \pm 0.9	62.4 \pm 0.5	61.8 \pm 2.2
3-50	3	18.8 \pm 2.0	72.7 \pm 3.5	72.9 \pm 3.2
7-50	3	20.5 \pm 3.4	72.2 \pm 5.8	73.7 \pm 5.5
14-50	3	18.8 \pm 1.5	72.1 \pm 2.7	72.4 \pm 2.5
1-80	3	18.7 \pm 1.7	96.5 \pm 0.4	96.5 \pm 0.4
3-80	3	20.7 \pm 1.0	94.3 \pm 0.3	99.1 \pm 1.6
7-80	3	24.4 \pm 7.9	84.3 \pm 7.0	85.9 \pm 5.9
14-80	3	22.7 \pm 2.7	92.9 \pm 1.1	95.5 \pm 0.5

organic content versus seston concentration (mg l^{-1}) and seston organic level is shown in Figure 10.

The non-parametric two-factor ANOVA (an extension of the single factor Kruskal-Wallis test) on faeces POM found no significant concentration effect ($F = 0.64$, $df = 3$, $P = 0.594$), a significant POM effect ($F = 7.09$, $df = 2$, $P = 0.004$) and a significant interaction effect ($F = 2.83$, $df = 6$, $P = 0.033$). Faeces percent POM was independent of seston concentration (Figure 10A).

The mean faeces organic contents for the 50 and 80 % organic levels were not significantly different from each other, but these two groupings were significantly higher than the mean faeces organic content for the 25 % organic diets (Table 12). The trend, therefore, is that the mean faeces organic content (%) increased slightly with increasing seston POM between 25 and 50 % POM and then became independent of seston POM (Figure 10B). The ANOVA interaction effect means that the effect of seston POM was not independent of the presence of a particular level of seston concentration. The interaction effect can be seen in both Figures 10A and 10B.

Figure 10. A) Faeces percent POM (%) versus seston concentration (mg l^{-1}). B) Faeces percent POM (%) versus seston POM (%).

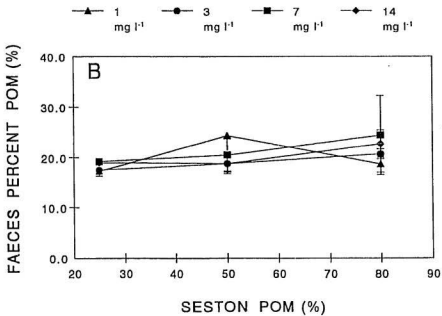
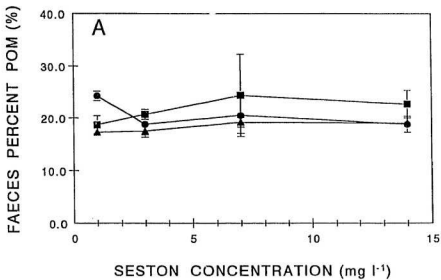


Table 12. Student Newman-Keuls test for faeces organic content, absorption efficiency and corrected absorption efficiency.

SNK grouping for mean faeces organic content by conc. *	SNK grouping for mean faeces organic content by POM *	SNK grouping for mean AE by conc. *	SNK grouping for mean corrected AE by conc. *
NSD	80 A A 50 A 25 B	NSD	NSD

N.B. SNK = Student Newman-Keuls test; conc. = concentration;
NSD = No significant difference between means.

* Mean rates are ranked by diet concentration and percent
POM from highest to lowest in descending order. Diets
with the same letter are not significantly different.

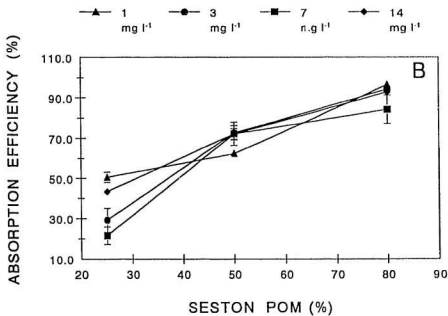
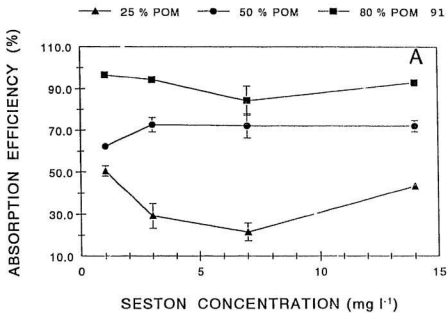
3.3.1.2. Absorption Efficiency

Two sets of absorption efficiency values were calculated for scallops from each experimental diet. The first was calculated using the mean percent POM of the seston and is termed the absorption efficiency (AE). The second was calculated using the mean total percent POM ingested after selection through pseudofaeces production was accounted for, and is termed the corrected absorption efficiency (AEC).

The mean absorption efficiencies (AE) for each diet ranged from $21.5 \pm 4.3 \%$ at the 7-25 diet to 96.5 ± 0.4 at the 1-80 diet (Table 11). Mean absorption efficiency (%) versus seston concentration (mg l^{-1}) and seston POM level (%) is shown in Figures 11A and 11B respectively.

The one way ANOVA on AE found no concentration effect ($F = 0.46$, $df = 3$, $P = 0.715$). The trend is that the mean absorption efficiency was independent of seston concentration for all three organic levels (Figure 11A). Mean absorption efficiency (%) increased with increasing seston quality for all four concentration levels (Figure 11B). This trend can be explained by the relative independence of faeces organic content versus seton POM (Figure 10B).

Figure 11. A. Absorption efficiency (%) versus seston concentration (mg l^{-1}). B) Absorption efficiency (%) versus seston POM (%).



The mean corrected absorption efficiencies (%) ranged from 16.6 ± 1.7 % at the 7-25 diet to 99.1 ± 1.6 at the 3-80 diet (Table 11). The one way ANOVA found no concentration effect ($F = 0.42$, $df = 3$, $P = 0.742$). The results of the SNK test for concentration for the corrected absorption efficiencies (AEC) were the same as for the uncorrected absorption efficiencies (AE) (Table 12). Therefore, the same trends were observed for the standard AE and AEC.

3.3.1.3. Absorbed Ration

The ingestion rates ($\text{mg h}^{-1} \text{g}^{-1}$) for each scallop were converted to Joules h^{-1} by multiplying by the grand mean energy content (Joules mg^{-1}) for the respective organic level of each diet mixture. For example, all ingestion rates ($\text{mg h}^{-1} \text{g}^{-1}$) in the four 25 % organic level concentrations were multiplied by the overall mean energy of seston of 4.14 (Joules mg^{-1}) from Table 4. For instance, a scallop fed the diet mixture of 1-25 had an ingestion rate of $6.67 \text{ mg h}^{-1} \text{g}^{-1}$ this value was multiplied by 4.14 Joules mg^{-1} to give an ingestion rate of 27.61 Joules $\text{h}^{-1} \text{g}^{-1}$. Each scallop's ingestion rate (Joules $\text{h}^{-1} \text{g}^{-1}$) was then multiplied by the mean corrected absorption efficiency for that diet mixture (Table 11) to obtain absorption rate (Joules $\text{h}^{-1} \text{g}^{-1}$). Active and routine values were calculated for both ingestion and

absorption in order to calculate active and routine scope for growth (Section 3.5. below).

3.3.2. Oxygen Consumption Rate

The mean oxygen consumption rates for each diet mixture ranged from a minimum of 0.223 ± 0.059 and 0.223 ± 0.060 at the 1-25 and 14-80 diets respectively, to a maximum of 0.335 ± 0.168 at the 1-50 diet (Table 13). Mean oxygen consumption rate versus seston concentration (mg l^{-1}) and seston POM (%) are shown in Figures 12A and 12B respectively.

The non-parametric two-factor ANOVA revealed no significant concentration effect ($F = 0.42$, $df = 3$, $P = 0.660$), no significant POM effect ($F = 1.12$, $df = 2$, $P = 0.347$) and no significant interaction effect ($F = 1.10$, $df = 6$, $P = 0.372$). The trend, therefore, is that mean oxygen consumption rate at 12°C was independent of both seston concentration and seston organic level (Figures 12A and 12B).

3.3.3. Ammonia Excretion Rate

Mean ammonia excretion rates ($\mu\text{g NH}_4\text{-N h}^{-1} \text{g}^{-1}$) ranged from a minimum of 17.9 ± 4.27 for the 3-50 diet to a maximum 34.6 ± 7.02 for the 7-50 diet (Table 14). Mean ammonia excretion rates versus seston concentration (mg l^{-1}) and

Table 13. Mean oxygen consumption rate (mls O_2 h^{-1} g^{-1}).

Experimental diet mixture (mg l^{-1} POM)	N	Mean oxygen consumption rate (mls O_2 h^{-1} g^{-1}) \pm s.d.
1-25	7	0.223 \pm 0.059
3-25	5	0.301 \pm 0.075
7-25	7	0.267 \pm 0.042
14-25	7	0.293 \pm 0.116
1-50	7	0.335 \pm 0.168
3-50	7	0.247 \pm 0.045
7-50	7	0.309 \pm 0.118
14-50	7	0.224 \pm 0.042
1-80	7	0.243 \pm 0.076
3-80	7	0.229 \pm 0.059
7-80	7	0.292 \pm 0.102
14-80	7	0.223 \pm 0.060

Figure 12. A) Oxygen consumption rate ($\text{ml O}_2 \text{ h}^{-1} \text{ g}^{-1}$) versus seston concentration (mg l^{-1}). B) Oxygen consumption rate ($\text{ml O}_2 \text{ h}^{-1} \text{ g}^{-1}$) versus seston POM (%).

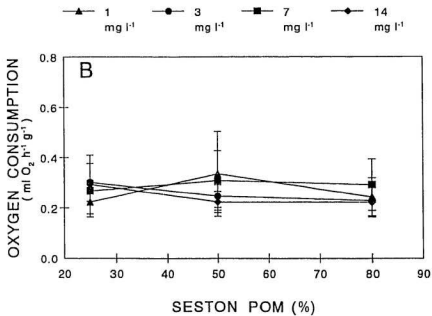
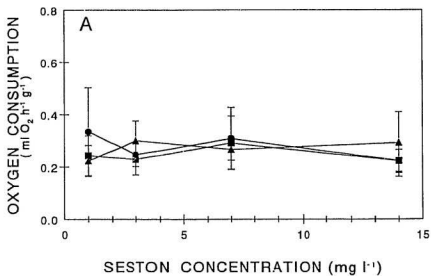


Table 14. Mean ammonia excretion rate ($\mu\text{g NH}_4\text{-N h}^{-1} \text{ g}^{-1}$).

Experimental diet mixture (mg l ⁻¹ POM)	N	Mean ammonia excretion rate ($\mu\text{g NH}_4\text{-N h}^{-1} \text{ g}^{-1}$) \pm s.d.
1-25	7	26.0 \pm 8.99
3-25	7	29.5 \pm 11.7
7-25	7	24.1 \pm 4.01
14-25	7	19.6 \pm 7.25
1-50	7	19.0 \pm 9.15
3-50	7	17.9 \pm 4.27
7-50	6	34.6 \pm 7.02
14-50	7	25.6 \pm 6.64
1-80	7	26.4 \pm 16.6
3-80	7	20.6 \pm 1.63
7-80	7	23.8 \pm 4.87
14-80	7	23.8 \pm 7.37

seston POM (%) are shown in Figures 13A and 13B respectively.

A non-parametric two-factor ANOVA revealed a slight concentration effect ($F = 2.87$, $df = 3$, $P = 0.0436$), no significant POM effect ($F = 0.31$, $df = 2$, $P = 0.734$), and a significant interaction effect ($F = 3.32$, $df = 6$, $P = 0.006$). Even though the two way model found a slight concentration effect, the SNK test for concentration found all of the mean ammonia excretion rates for all four concentration levels not significantly different from one another (not shown). The mean ammonia excretion rate appeared to be independent of both seston concentration and seston POM (Figures 13A and 13B). The ANOVA interaction effect indicates that the effect of concentration was not independent of the presence of a particular level of POM. The interaction effect can be seen in both Figures 13A and 13B.

3.4. Integration of Energy Gain and Losses - Scope for Growth

Once the energy gains and the energy losses have been converted to common energy equivalents, the scope for growth for a particular scallop can be determined. The mean active and routine scope for growth values for each diet mixture are shown in Table 15. Mean active scope for growth (Joules

Figure 13. A) Ammonia excretion rate ($\mu\text{g NH}_4\text{-N h}^{-1} \text{g}^{-1}$) versus seston concentration (mg l^{-1}). B) Ammonia excretion rate ($\mu\text{g NH}_4\text{-N h}^{-1} \text{g}^{-1}$) versus seston POM (%).

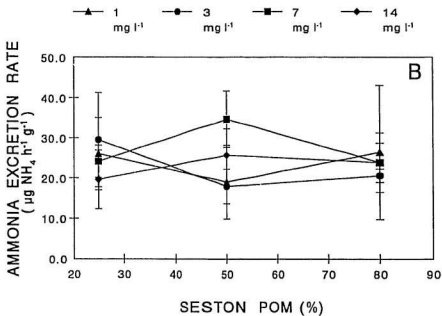
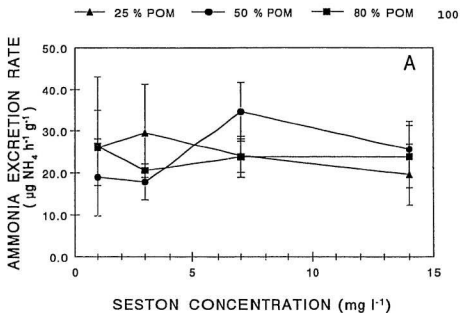


Table 15. Mean active and mean routine scope for growth (Joules h⁻¹ g⁻¹).

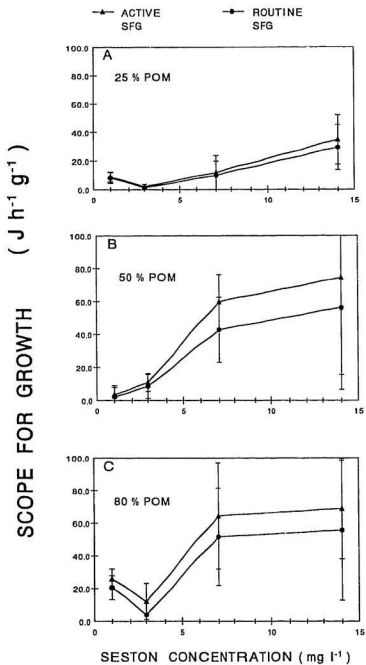
Exp. diet mixture (mg l ⁻¹ POM)	N	Mean active scope for growth (Joules h ⁻¹ g ⁻¹) ± s.d.	Mean routine scope for growth (Joules h ⁻¹ g ⁻¹) ± s.d.
1-25	7	8.89 ± 3.49	8.14 ± 3.91
3-25	4	2.10 ± 2.17	1.25 ± 2.38
7-25	7	11.09 ± 11.87	9.90 ± 9.91
14-25	7	34.85 ± 17.29	29.45 ± 15.66
1-50	7	3.41 ± 5.46	2.23 ± 5.64
3-50	7	10.78 ± 5.49	8.37 ± 7.27
7-50	7	59.93 ± 16.34	42.88 ± 19.76
14-50	7	74.49 ± 59.02	56.25 ± 49.79
1-80	7	25.88 ± 6.04	20.63 ± 7.27
3-80	6	12.15 ± 11.16	4.03 ± 9.04
7-80	7	64.43 ± 32.44	51.72 ± 29.76
14-80	7	68.98 ± 30.70	55.79 ± 42.78

$\text{h}^{-1} \text{g}^{-1}$) ranged from a minimum of 2.10 ± 2.17 at the 3-25 diet to a maximum of 74.5 ± 59.0 at the 14-50 diet (Table 15). Mean routine scope for growth ($\text{Joules h}^{-1} \text{g}^{-1}$) ranged from a minimum of 1.25 ± 2.38 at the 3-25 diet to a maximum of 56.2 ± 49.8 at the 14-50 diet. Estimates of mean active and routine scope for growth ($\text{Joules h}^{-1} \text{g}^{-1}$) versus seston concentration (mg l^{-1}) and seston POM (%) are shown in Figure 14. The trend is that mean scope for growth increased with increasing concentration (Figure 14). Overall, the trends for routine scope for growth with increasing particle concentration and diet quality were the same as those for active scope for growth. Scope for growth appeared to increase with increasing seston quality (Table 15). Interestingly, mean active scope for growth for the 50 and 80 % POM diets were similar at concentrations 3 mg l^{-1} and greater (Table 15 and Figure 14).

3.5. Scallop Conditioning Experiment

When data are collected using repeated measures design they should be tested for symmetry (similar to normality) using Mauchly's criterion Test (Potvin et al. 1990). With the exception of the data for pseudofaeces production, all other data in this section met this assumption (see Section

Figure 14. Scope for growth ($J\ h^{-1}\ g^{-1}$) versus seston concentration ($mg\ l^{-1}$) for: **A)** the 25% POM diet mixtures; **B)** the 50% POM diet mixtures; and **C)** the 80% POM diet mixtures.



3.6.C. below); therefore, univariate ANOVARS were used to test the data.

3.5.1 Clearance Rate

Mauchly's criterion was met for all CR and ingestion rate data (Mauchly's criterion > 0.505 , $P > 0.248$). The mean active CR for the maintained group ranged from 1.68 ± 0.54 to 0.56 ± 0.29 ($l\ h^{-1}\ g^{-1}$), while CR for the supplemented group ranged from 2.66 ± 0.57 to 1.11 ± 0.57 (Figure 15A). The mean routine CR for the maintained group ranged from 1.32 ± 0.59 to 0.42 ± 0.25 ($l\ h^{-1}\ g^{-1}$), while that for the fed or supplemented group ranged from 2.48 ± 0.44 to 1.13 ± 0.58 (Table 16).

There was a significant difference in active CRs ($l\ h^{-1}\ g^{-1}$) between the maintained and supplemented groups ($F = 13.83$, $df = 1$, $P = 0.003$), a significant time effect ($F = 20.90$, $df = 3$, $P < 0.001$), and no significant interaction effect ($F = 1.59$, $df = 3$, $P = 0.210$). The successive contrast of the means with time found that the mean active CR at time 0 was significantly greater than the mean rate at time 24 ($F = 33.99$, $df = 1$, $P < 0.001$); the mean rate at time 24 was not significantly different from the mean at time 48 ($F = 0.63$, $df = 1$, $P = 0.445$), and the mean rate at time 48 was significantly greater than the mean rate at time

Figure 15. A) Active clearance rate ($\text{l h}^{-1} \text{g}^{-1}$) versus time (hours). B) Pseudofaeces production rate ($\text{mg h}^{-1} \text{g}^{-1}$) versus time (hours).

▲ MAINTAINED

● SUPPLEMENTED

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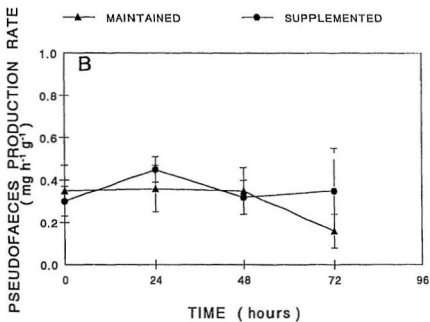
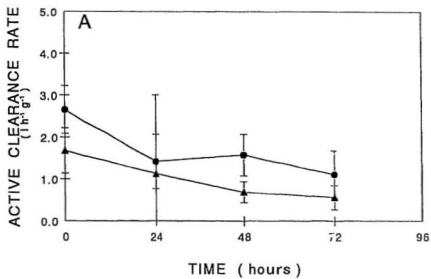


Table 16. Mean active and mean routine clearance rate ($l\ h^{-1}\ g^{-1}$) with time fed (hours) for the maintained (M) and supplemented (S) groups.

Time (h)	N M,S	Mean active clearance rate ($l\ h^{-1}\ g^{-1}$) \pm s.d.		Mean routine clearance rate ($l\ h^{-1}\ g^{-1}$) \pm s.d.	
		M	S	M	S
0	6,7	1.68 ± 0.54	2.66 ± 0.57	1.32 ± 0.59	2.48 ± 0.44
24	6,7	1.17 ± 1.88	1.42 ± 0.65	0.75 ± 0.33	1.15 ± 0.55
48	6,7	0.69 ± 0.25	1.58 ± 0.50	0.50 ± 0.26	1.33 ± 0.50
72	6,7	0.56 ± 0.29	1.11 ± 0.57	0.42 ± 0.25	1.13 ± 0.58

72 ($F = 5.41$, $df = 1$, $P = 0.040$). The slope of the supplemented group was -0.449 ($r^2 = 0.404$) and the slope of the maintained group was -0.3813 ($r^2 = 0.535$). Examination of Figure 15A suggested that mean active CR decreased between time 0 and time 24, and became independent of time between time 24 and time 72. The ANOVAR was run again for times greater than 0 and there was no time effect after 24 hours ($F = 2.94$, $df = 2$, $P = 0.074$). These results indicate that the mean active CR ($l\ h^{-1}\ g^{-1}$) decreased with increasing feeding time (hs) between time 0 and 24 and then became independent of feeding time between time 24 and 72 on the 3-80 mg l^{-1} diet mixture (Figure 15A). Also, the results showed that the supplemented scallops cleared particles at a greater rate than scallops that had been maintained. The same results were obtained when the identical analyses were performed on routine CRs (not shown).

3.5.2 Pseudofaeces

The mean pseudofaeces production rate ($mg\ h^{-1}\ g^{-1}$) for the maintained group ranged from 0.16 ± 0.08 to 0.35 ± 0.12 over the experimental period, while that for the supplemented group ranged from 0.30 ± 0.07 to 0.45 ± 0.06 (Table 17). The mean pseudofaeces production rates versus time for both groups are shown in Figure 15B.

Table 17. Mean pseudofaeces rate ($\text{mg h}^{-1} \text{g}^{-1}$) with time fed (hours) for the maintained (M) and the supplemented (S) groups.

Time (h)	N M,S	Mean pseudofaeces rate ($\text{mg h}^{-1} \text{g}^{-1}$) \pm s.d.	
		M	S
0	6,7	0.35 ± 0.12	0.30 ± 0.07
24	6,7	0.36 ± 0.11	0.45 ± 0.06
48	6,7	0.35 ± 0.11	0.32 ± 0.08
72	6,7	0.16 ± 0.08	0.35 ± 0.20

The data for pseudofaeces did not meet the univariate criteria so MANOVAR was conducted. There was no significant difference in the pseudofaeces production rate between maintained and supplemented scallop groups ($F = 1.23$, $df = 1$, $P = 0.290$), a significant time effect ($F = 5.00$, $df = 3$, $P = 0.026$) and no significant interaction effect ($F = 3.61$, $df = 3$, $P = 0.058$). The successive contrast found that the mean pseudofaeces production rates for time zero were significantly lower than the mean rates for time 24 ($F = 8.56$, $df = 1$, $P = 0.014$); the mean rates for time 24 were significantly higher than the mean rates for time 48 ($F = 6.22$, $df = 1$, $P = 0.030$) and the mean rates for time 48 were in turn significantly higher than the mean rates for time 72 ($F = 4.86$, $df = 1$, $P = 0.050$). The supplemented group had a slope of -0.007 ($r^2 = 0.004$) and the maintained group had a slope of -0.058 ($r^2 = 0.260$). Despite these low slope values, the MANOVAR results indicate that the mean pseudofaeces rate ($\text{mg h}^{-1} \text{g}^{-1}$) decreased with increasing time (hours) fed on the 3-80 diet mixture (Figure 15B). Also, the supplemented scallops produced more pseudofaeces than the maintained scallops.

3.5.3. Ingestion Rate

The mean active ingestion rate for the maintained group ranged from 2.91 ± 1.02 to 0.92 ± 0.48 at time 0 during the experiment, while that for the supplemented group ranged from 4.86 ± 1.08 to 1.97 ± 0.92 (Figure 16A). The mean routine ingestion rate ($\text{mg h}^{-1} \text{g}^{-1}$) for the maintained group ranged from 2.20 ± 1.20 to 0.65 ± 0.42 for time 0 during the experiment while the supplemented group ranged from 4.51 ± 0.82 to 1.83 ± 0.95 for time 0 (Table 18).

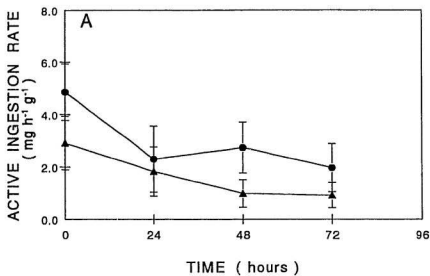
There was a significant difference in active ingestion rate ($\text{mg h}^{-1} \text{g}^{-1}$) between the maintained and supplemented scallop groups ($F = 14.50$, $df = 1$, $P = 0.003$), a significant time effect ($F = 21.53$, $df = 3$, $P < 0.001$), and no significant interaction effect ($F = 2.19$, $df = 3$, $P = 0.107$). The successive contrast for mean active ingestion rate with time found that the mean ingestion rates for time zero were significantly higher than those for time 24 ($F = 33.92$, $df = 1$, $P < 0.001$), but the mean rates for time 24 were not significantly different from those for time 48 ($F = 0.34$, $df = 1$, $P = 0.572$), and the mean rates for time 48 were in turn not significantly different from the mean rates for time 72 ($F = 4.23$, $df = 1$, $P = 0.064$). Data in Figure 16A suggest that ingestion is independent of time at times greater than zero. This was indeed confirmed in an ANOVAR

Figure 16. A) Active ingestion rate ($\text{mg h}^{-1} \text{g}^{-1}$) versus time (hours). B) Faeces percent POM (%) versus time (hours).

—▲— MAINTAINED

—●— SUPPLEMENTED

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—▲— MAINTAINED

—●— SUPPLEMENTED

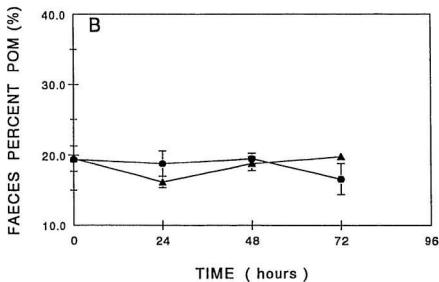


Table 18. Mean active and mean routine ingestion rate ($\text{mg h}^{-1} \text{g}^{-1}$) with time fed (hours) for the maintained (M) and supplemented (S) groups.

Time (h)	N M,S	Mean active ingestion rate ($\text{mg h}^{-1} \text{g}^{-1}$) \pm s.d.		Mean routine ingestion rate ($\text{mg h}^{-1} \text{g}^{-1}$) \pm s.d.	
		M	S	M	S
0	6,7	2.91 ± 1.02	4.86 ± 1.08	2.20 ± 1.12	4.51 ± 0.82
24	6,7	1.83 ± 0.94	2.30 ± 1.26	1.09 ± 0.59	1.78 ± 1.09
48	6,7	0.99 ± 0.53	2.74 ± 0.97	0.63 ± 0.55	2.25 ± 0.98
72	6,7	0.92 ± 0.48	1.97 ± 0.92	0.65 ± 0.42	1.83 ± 0.95

for times greater than zero, which found no time effect after 24 hours of feeding ($F = 2.14$, $df = 2$, $P = 0.141$). The slope for the supplemented group was -0.866 ($r^2 = 0.403$) and the slope for the maintained group was -0.681 ($r^2 = 0.503$). The results indicate that mean active ingestion rate ($\text{mg h}^{-1} \text{g}^{-1}$) decreased with increasing feeding time (hours) between time 0 and time 24, and then became independent of feeding time between time 24 and time 72 (Figure 16A). These results showed that the supplemented scallops ingested particles at a greater rate than did scallops that had been maintained. The same results were obtained for routine ingestion rates when the identical analyses were performed on routine ingestion (not shown).

3.5.4. Faeces

There were only two samples of faecal material available from each experimental group; therefore, the sphericity test could not be carried out and no statistical analysis performed on either percent POM in the faeces or on absorption efficiency. Therefore only the overall trends can be discussed. The mean faeces organic content for the maintained group ranged from 15.4 to 21.3 over the experimental period, while that for the supplemented group ranged from 14.4 to 20.6 (Table 19; Figure 16B). A linear

Table 19. Faeces organic content (%), absorption efficiency (%) and corrected absorption efficiency (%) with time fed (hours) for the maintained (M) and the supplemented (S) groups.

Time (h)	N M,S	Faeces organic content (%)		Absorption efficiency (%)		Corrected absorption efficiency* (%)	
		M	S	M	S	M	S
0	2,2	17.7, 21.3	19.1, 19.7	97.7, 98.1	98.9, 98.9	98.6, 99.2	98.1, 98.3
24	2,2	15.4, 17.0	17.0, 20.6	98.2, 98.4	97.6, 98.2	99.0, 100.0	99.1, 99.7
48	2,2	17.8, 19.8	18.7, 20.3	93.9, 100.0	97.7, 97.9	100.0, 100.0	98.1, 98.3
72	2,2	19.8, 19.8	14.4, 18.8	97.8, 97.8	97.6, 98.4	100.0, 100.0	100.0, 100.0

regression for faeces organic content against time found a very slight positive slope for the maintained group ($b = 0.365$) and a very slight negative slope for the supplemented group ($b = -0.850$). The overall trend appears to be that faeces organic content (%) for both groups did not substantially change with increasing feeding time on the 3-80 diet mixture (Figure 16B).

3.5.5. Absorption Efficiency and Absorption Efficiency Corrected

The mean absorption efficiency for the maintained group ranged from 93.9 to 100.0 over the experimental period, while the mean absorption efficiency for the supplemented group ranged from 97.6 to 98.9 (Table 19). A linear regression of absorption efficiency against time found a very slight negative slope for the maintained group ($b = -0.050$) and a very slight positive slope for the supplemented group ($b = 0.120$). However, the overall trend appears to be that absorption efficiency (%) does not change substantially with increasing exposure to the 3-80 diet mixture.

The mean corrected absorption efficiencies for the maintained and fed groups were slightly higher than the uncorrected values. Similar results for the regression analysis lead to the same conclusion that corrected

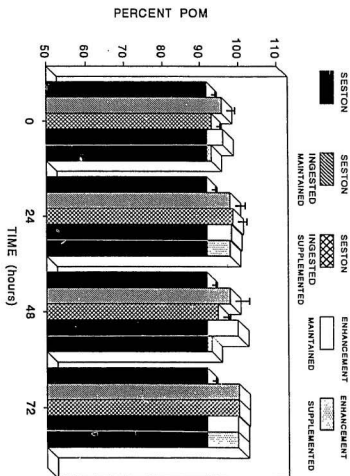
absorption efficiency did not change with increasing exposure time.

3.5.6. Percent Enhancement of Food

The total percent POM ingested and the percent enhancement of the diet was calculated as above (Section 3.2.3.1 above) for both groups (maintained and supplemented) versus time (hours) and is shown in Figure 17. The actual obtained percent POM of the diet of C. muelleri fed to the scallops was determined to be 90 % POM (Figure 17). Both groups of scallops enhanced the material to be ingested for all four time periods. The percent enhancement of the diet mixture increased with increasing time (Figure 17). Because only two samples of faecal material were available (Section 3.5.4. above) no statistical analysis was performed on the percent enhancement of food.

Figure 17. Seston POM (%), actual seston ingested by scallops (both maintained and supplemented, corrected for alteration of seston POM by pseudofaeces production) (%), and percent enhancement of the seston (%) by scallops (both maintained and supplemented) versus time (hours).

90 % POM DIET



4. Discussion

4.1. Experimental Conditions

With the exception of the diets consisting of 80% POM (pure cultured diatoms) the experimental diet mixtures used in this study are within the range of environmental conditions that P. magellanicus is exposed to in eastern Newfoundland (MacDonald and Thompson 1986). The experimental diets consisted of relatively small particles of C. muelleri and silicon dioxide (i.e 4-6 μm). These particles are readily cleared and ingested by this species (Cranford and Grant 1990) and are within the size range of particles that routinely dominate seston in the natural environment. Most post-settlement stages of suspension feeding bivalves are capable of retaining particles larger than 3-4 μm with 100 % efficiency (Bricelj and Shumway 1991). Juvenile P. magellanicus are capable of selecting certain particles, based solely on size, from algal mixtures made up of different sizes of particles (Lesser et al. 1991). The organic and inorganic components of the diets in my study were chosen to be approximately the same size, thus reducing the possibility that the different particles were selected or rejected based on size alone.

4.2. Estimating Energy Uptake

4.2.1. Clearance Rate

Scallop clearance rates in this study ranged from a high of 5.61 ± 1.55 to a low of 0.49 ± 0.36 ($l\ h^{-1}\ g^{-1}$) over seston concentrations from 1 to $14\ mg\ l^{-1}$ (ca. 8,000- 161,000 part. ml^{-1}) and diet qualities between 23 and 87 % POM (Figures 3A-B). These rates are comparable to the values between reported by MacDonald (1984) for much larger adult P. magellanicus in eastern Newfoundland feeding on natural seston. Grant and Cranford (1991) also studied feeding activity in adult P. magellanicus ($12^{\circ}\ C$) at concentrations of 1 to $2\ mg\ l^{-1}$ using diets consisting of aged kelp, resuspended sediment, Isochrysis galbana and Chaetoceros gracilis. When Grant and Cranford's (1991) data were converted to weight specific values for a 1 g scallop using MacDonald and Thompson's (1986) weight exponent, CRs ranged from 1.5 to $5.83\ l\ h^{-1}\ g^{-1}$. Their values of 4.3 to $5.6\ l\ h^{-1}\ g^{-1}$ recorded for low concentrations, approximately 1 to $3\ mg\ l^{-1}$, compare favourably with my data.

Clearance rates for diets consisting of cultured algae were comparable to those reported in the literature. Palmer (1980) found CRs for Argopecten irradians concentricus fed Thalassiosira pseudonana of $4.0\ l\ h^{-1}\ g^{-1}$ (50,000-340,000 cells ml^{-1}) and $5.7\ l\ h^{-1}\ g^{-1}$ when fed Dunaliella tertiolede

(10,000-30,000 cells ml⁻¹) (temp. = 12° C). A.i. irradians fed T. weissflogii at cell concentrations of 1,200, 4,800 and 12,000 cells ml⁻¹ (Temp. = 22° C) had CRs of 10.3, 4.7 and 1.4 l h⁻¹ g⁻¹, respectively (Bricelj and Kuenstner 1989). McKlusky (1973) found CRs of 1.6, 3.2 and 5.9 l h⁻¹ g⁻¹ at temperatures of 5, 10, and 20 ° C respectively for Chlamys opercularis fed D. euchlora at concentrations between 8,000 and 10,000 cells ml⁻¹.

Results from previous feeding studies using similar sized mussels and clams and diets that consisted of mixtures of algal cells and silt compared favourably to the present study. Bayne et al. (1987) found that CRs (not standardized for weight) of M. edulis ranged from 1.1 - 4.0 l h⁻¹ for diets ranging from 6.8 - 110.9 mg l⁻¹ and POM that ranged from 9.2 - 35.8 %. M. edulis feeding on 10,000 cells ml⁻¹ of Phaeodactylum tricornutum, and silt concentrations ranging from 0-55 mg l⁻¹, had CRs of 4.0 l h⁻¹ (Kjørboe et al. 1980). Finally, Bricelj and Malouf (1984) found CRs ranging from 1.5 - 5.5 l h⁻¹ g⁻¹ for the hard clam, Mercenaria mercenaria, feeding on Pseudoisochrysis paradoxa (50,000-150,000 cells ml⁻¹) and bottom sediments (0-44 mg l⁻¹). In general, CRs in my study are comparable to published values for similar sizes of other species studied under similar rations.

Clearance rates decreased markedly as particle concentration increased, particularly between 1 and 3 mg l⁻¹, before appearing to become relatively independent of particle concentration between 3 and 14 mg l⁻¹ (Figures 3A and 4A). Strong inverse relationships between CR and algal concentration have also been observed for other species of pectinids (Palmer 1980, Bricelj and Kuenstner 1989, Cahalan et al. 1989). Bricelj and Kuenstner (1989) found an 85 % decrease in CR for the bay scallop with a 10-fold increase in the concentration of T. weissflogii (1,200-12,000 cells ml⁻¹). Similar reductions (85 % and an 88 % reduction in active and routine CR, respectively) were observed for P. magellanicus exposed to a 9-fold increase in the number of C. muelleri (ca. 18,000-161,000 cells ml⁻¹, Table 2) during these experiments. Exposure to mixtures of algae and silica (25 and 50 % POM) resulted in reductions of active and routine CRs (as concentrations increased) of 70 % and 72.0 % respectively for the 25 % POM diets and 58 and 60 % respectively for the 50 % POM diets. These values are similar to estimates reported by Cahalan et al. (1989) who reported a 56 % reduction in CR for the bay scallop with an increase in I. galbana between 7,500-68,000 cells ml⁻¹.

Strong inverse relationships between CR and increasing seston concentration have been well documented for bivalves

in general, particularly clams and mussels (Foster-Smith 1975, Winter 1976; 1978, Widdows et al. 1979, Bayne and Newell 1983, Bricelj and Malouf 1984, Malouf and Bricelj 1989, Navarro et al. 1992). Bricelj and Malouf (1984), for example, found CRs in M. mercenaria, fed on mixed suspensions of P. paradoxa (50,000-150,000 cells ml⁻¹) and bottom sediments (0-44 mg l⁻¹), decreased 0.08 l h⁻¹ g⁻¹ (1.3 %) for every 1 mg l⁻¹ increase in sediment load. In contrast, some authors have found CR independent of algal concentration over narrow ranges (1,500-30,000 cells ml⁻¹ P. tricornutum) (Rissgard and Randlov 1981). Others have found no change in CR in M. edulis over ranges of natural seston (ca. 7-110 mg l⁻¹, 7-55 % organic matter) (Bayne et al. 1987). The addition of small amounts of silt (5 mg l⁻¹) has produced increases in CR in M. edulis when compared to CRs for mussels fed pure algal suspension (Kjørboe et al. 1981). There do not seem to be any clear trends in feeding activity related to changing particle concentrations and the observed responses may depend very much on such factors as the species being tested, sampling location, concentration and type of particle tested.

Fewer studies have examined the effects of varying seston quality on bivalve CR. Clearance rate (active and routine) decreased between 25 and 50 % POM and then became

independent of seston quality between the 50 and 80 % POM diets (Figure 3B). Notably, CRs were highest at the poorest quality diet (25 % POM) and lowest at the highest quality diet (80 % POM) (Figure 3B). Cranford and Grant (1990) found the opposite trend for adult P. magellanicus with the highest CRs occurring on two algal species C. gracilis and I. galbana (POM ca. 78-85 %) versus lower CRs on resuspended sediments (POM ca. 30 %). However, their particle concentrations encompassed a narrow range (0.5-2.5 mg l⁻¹) of low concentrations and a different response may have been observed at higher concentrations. Ward et al. (1992) reported that this species of scallop could be stimulated to clear inert particles more rapidly if they were treated with algal metabolites. This procedure appeared to improve the quality of the particles and made them more attractive to the scallops. Nevertheless, as part of its feeding strategy when fed a poorer quality diet (i.e. 25 % POM), a scallop may have to clear more of the material per unit time in order to obtain a similar amount of energy available from feeding on a better quality diet (i.e. 80 % POM).

4.2.2. Pseudofaeces

Above a threshold particle concentration, bivalves often produce pseudofaeces to reject excess particles and regulate ingestion. Griffiths and Griffiths (1987) reported that threshold concentrations of suspended material that initiate pseudofaeces production for most species of bivalves lie between 1 and 6 mg l⁻¹ dry weight of seston. In my study, pseudofaeces was produced at all diet mixtures (1-14 mg l⁻¹) representing a rather low threshold of approximately 1 mg l⁻¹ for juvenile P. magellanicus.

The production of pseudofaeces (part. h⁻¹ g⁻¹) increased with increasing seston concentration, oscillated with increasing seston quality (i.e. lowest at the 50 % POM diets), and only represented a maximum of 7.2 ± 6.9 % of the total material cleared (Figure 4A-B). Similar trends were observed for pseudofaeces production in mg h⁻¹ g⁻¹ with the exception that the percentage of cleared material rejected reached 32%. The amount of material rejected is comparable to results of Bricelj and Kuenstner (1989) who found the bay scallop A. irradians rejected up to 25-35 % of the algal cells when exposed to blooms of Aereococcus anophagefferens (ca. $0.55-1.67 \times 10^6$ cells ml⁻¹ = 2.4-6.4 mg l⁻¹ dry wt. of algae).

The pseudofaeces production threshold of 1 mg l^{-1} (ca. 8,000 cells ml^{-1} C. muelleri) is lower than the value of 6 mg l^{-1} reported by Palmer (1980) for the bay scallop feeding on mixed phytoplankton diets in the range of $0.08\text{--}10.89 \text{ mg l}^{-1}$, but it agrees favourably with published results for adult P. magellanicus and A. islandica ($10,000 \text{ cells ml}^{-1}$) (Shumway et al. 1985). In contrast, pseudofaeces production was not observed for juvenile P. magellanicus fed mixed phytoplankton concentrations of $10,000 \text{ cells ml}^{-1}$ (Lesser et al. 1991). Also, MacDonald and Thompson (1986) did not observe large amounts of pseudofaeces being released by adult sea scallops feeding on low concentrations of natural seston in eastern Newfoundland.

Pseudofaeces production in bivalves has routinely been found to increase with increasing seston concentration (Foster-Smith 1975, Widdows et al. 1979, Kjørboe et al. 1980, Bayne and Newell 1983, Bricelj and Malouf 1984, Robinson et al. 1984, Griffiths and Griffiths 1987). Widdows et al. (1979) reported that pseudofaeces production rate increased at a reducing rate for M. edulis with increasing seston concentration (ca. $2.6\text{--}5.0 \text{ mg l}^{-1}$) depending on body size. The surf clam, Spisula solidissima, increased its pseudofaeces production rate when fed a constant concentration of microalgae (0.025 mg l^{-1}) and increasing

clay concentrations (0, 100, 500 and 1000 mg l⁻¹) (Robinson et al. 1983). There is very little information available on the relationships between pseudofaeces production and seston quality.

Scallops are thought to regulate their ingestion rate at high particle concentrations primarily by reducing their CR rather than by increasing their pseudofaeces production (Bricelj and Shumway 1991). Pseudofaeces production rate is ultimately a function of CR and will not only differ between species but respond differently to the nature and density of material in suspension (Griffiths and Griffiths 1987). The tendency for pseudofaeces production to plateau at high suspension loads is caused by the tendency for CR to decline at high food concentration (Griffiths and Griffiths 1987). In the present study, a plateau in pseudofaeces production was not observed, possibly because much lower concentrations were used than in other published studies. Nevertheless, this species has the capability of increasing pseudofaeces production and reducing CRs with increasing seston in order to regulate ingestion.

4.2.2.1. Selection Process

Pre-ingestive particle selection is theoretically possible for bivalves only when pseudofaeces are produced.

However, selection on the gill (i.e. without the production of pseudofaeces) has been reported for Ostrea edulis (Shumway et al. 1985) and M. edulis (Newell et al. 1989) when sophisticated flow cytometry techniques have been used. Natural suspensions often consist predominately of inorganic material that may dilute the nutritional organic fraction, and hence decrease the energy value of the food (Kiørboe et al. 1981). However, if a bivalve has the capability of rejecting inorganic particles through pseudofaeces production, thereby improving the ratio of the POM to be ingested, it could reduce or potentially eliminate any dilution effect by PIM. Recent studies have found that some species of bivalves can selectively ingest algae and reject particles of poor nutritive value (i.e. sediment particles) (Kiørboe et al. 1980, Kiørboe and Møhlenberg 1981, Newell and Jordan 1983, Shumway et al. 1985, Newell et al. 1989, Ward and Targett 1989, Lesser et al. 1991, Iglesias et al. 1992).

Kiørboe and Møhlenberg (1981) have shown that the efficiency of selection in marine bivalves is quite variable among different species and may be related to the size of the labial palps. They determined the efficiency of particle selection of ten species of suspension feeding bivalves fed mixed algal-sediment suspensions (10-30,000 cells ml⁻¹ P.

triconutum) and suspended bottom material (10-20 mg l⁻¹). The selection efficiency was estimated from the ratio of chlorophyll-a to dry weight in suspended material and pseudofaeces. Kiørboe et al. (1980) concluded that M. edulis was well adapted to silt concentrations up to 55 mg l⁻¹ and could actively select particles of high food value (P. tricornutum) over those of lower food value (silt). Newell and Jordan (1983) have shown that Crassostrea virginica, an estuarine species, also has a well developed ability to preferentially ingest various types of organic material and reject other particles (PIM) in pseudofaeces. The only pectinid tested, Aequipecten opercularis, showed an intermediate selection efficiency (= 5.4) versus 15.8 for S. subtruncata and 2.9 for M. edulis from a low turbidity environment (Kiørboe and Møhlenberg 1981). The positive percent enhancement in the present study (range = 5.0-13.9) compares favourably to that reported by Kiørboe and Møhlenberg (1981).

With the exception of Iglesias et al. (1992), the above studies demonstrating selective capabilities of bivalves did so using qualitative analysis of pseudofaeces and seston samples, with little regard for the quantity of pseudofaeces produced. They demonstrated that bivalves had the capability to select, but without consideration of the amount of

pseudofaeces produced it is difficult to determine whether there was a meaningful improvement in the quality of the material ingested on longer time scales. For example, it is possible for an animal to greatly alter, in terms of percent POM or chlorophyll ratio, a small amount of pseudofaeces but have very little impact on how much it ingested over a 24 hour period (MacDonald and Ward 1994, in press).

Significant enhancement of the ingested ration, taking into consideration the quality and the quantity of the pseudofaeces produced and equating it to amount of material cleared, was observed in five out of the ten diet mixtures in which pseudofaeces was produced. Positive percent enhancement was found for scallops fed 50 and 80 % POM diets. Interestingly, even scallops fed the 80 % POM diets (*C. muelleri* only) could improve the organic content of their diets (Table 8). Scallops fed the highest concentration and lowest quality (i.e. 14-25) diet mixture actually made the quality of the material to be ingested worse (-6.0 ± 3.8 %, Table 8). It seems unusual that this species has the ability to improve the diet POM when it is already very good quality, but not the ability to improve the diet POM it under poor food conditions. Newell et al. (1989) also reported that the selective capabilities of *Mytilus edulis* were not as efficient when food quality was low and PIM exceeded 80%. Scallops in eastern Newfoundland

are not typically found in the same type of turbid environments that mussels and oysters are and therefore may not have evolved as efficient selection mechanisms as these other species.

4.2.3. Ingestion Rate

Ingestion rates were expressed in both $\text{part. h}^{-1} \text{g}^{-1}$ and $\text{mg h}^{-1} \text{g}^{-1}$ because there is a dichotomy in the literature in the units in which ingestion rate is commonly expressed. This lack of standardization may contribute to some of the discrepancies observed for the same species studied under similar circumstances. Most earlier studies using monocultured algae express ingestion rate in $\text{particles h}^{-1} \text{g}^{-1}$, whereas studies using diet mixtures or natural seston use $\text{mg h}^{-1} \text{g}^{-1}$. Ingestion rates (both active and routine) in my study ranged from 2.8 to $19.8 \times 10^7 \text{ part. h}^{-1} \text{g}^{-1}$, and previous studies using cultured algae ranged from 2 to $18.0 \times 10^7 \text{ part. h}^{-1} \text{g}^{-1}$. This includes ingestion rates of 1.2 to $2.4 \times 10^7 \text{ cells h}^{-1} \text{g}^{-1}$ and 0.3 to $1.5 \times 10^9 \text{ cells h}^{-1} \text{g}^{-1}$ (algal concentration range = 1.2×10^3 – 2×10^6) for the bay scallop fed algal diets of *T. weissflogii* and *A. anophagefferens* (Bricelj and Kreunster 1989). Foster-Smith (1975) also found similar (non-weight specific) ingestion rates (= 0.1 to $10 \times 10^7 \text{ cells h}^{-1}$) for similar sized *M. edulis* fed concentrations

of P. tricornutum ranging from ca. 25,000-800,000 cells ml⁻¹. However, the ingestion rates for the present study are higher than those observed for hard clams (range = ca. 1.5 to 4.8 x 10⁵ cells h⁻¹ g⁻¹) fed mixed suspensions of P. paradoxa (= 50,000-150,000 cells ml⁻¹) and bottom sediments (= 0-44 mg l⁻¹) (Bricelj and Malouf 1984).

Over the entire range of diets tested, ingestion rates (mg h⁻¹ g⁻¹, both active and routine) for P. magellanicus ranged from 1.0 to 24.8 mg h⁻¹ g⁻¹. Ingestion on diets consisting of only C. muelleri ranged from 1.0 to 8.7 mg h⁻¹ g⁻¹. These compare favourably to ingestion rates found by Palmer (1980) for the bay scallop (ca. 4-20 mg h⁻¹ g⁻¹) fed mixed algal suspensions ranging from 0.9 to 9.7 mg l⁻¹. Ingestion rates for adult P. magellanicus fed C. gracilis (8.8 to 9.5 mg h⁻¹ g⁻¹) and Tahitian Isochrysis (7.3 to 8.1 mg h⁻¹ g⁻¹) at concentrations of approximately 2 mg l⁻¹ were in the same range (Cranford and Grant 1990). When adults were fed 2 mg l⁻¹ of resuspended silt (1.4 to 2.6 mg h⁻¹ g⁻¹), their ingestion rates were much lower than rates observed (6.3 to 6.7 mg h⁻¹ g⁻¹) for juveniles exposed to the lowest concentration and poorest quality diet (i.e. 1 mg l⁻¹ at 25% POM). Similar rates of ingestion have been reported for Mytilus edulis by Bayne et al. (1989) and (Kjørboe et al. 1980).

Ingestion rate (particles $\text{h}^{-1} \text{g}^{-1}$), in my study, increased with increasing seston concentration. Ingestion rates in the bay scallop also increased with increasing concentrations of T. weissflogii and A. anophagefferens (1.2 to 12.0×10^4 cells ml^{-1} and 2 to 20×10^5 cells ml^{-1}), respectively (Bricelj and Kuenstner 1989). Alternatively, when ingestion rates were expressed in $\text{mg h}^{-1} \text{g}^{-1}$, they increased between 3 and 7 mg l^{-1} and then became independent of seston concentration between 7 and 14 mg l^{-1} . Foster-Smith (1975) also found ingestion in M. edulis to increase with rising algae concentration between $25,000$ and $200,000$ cells ml^{-1} before levelling off at concentrations between $200,000$ – $800,000$ cells ml^{-1} . Ingestion may decrease again at extremely high concentrations because the bivalve's filtering capability is saturated and pseudofaecal production is at a maximum (Widdows et al. 1979). Both types of responses, an increase or an increase then a plateau with increasing seston concentration have been observed in this study, and the response may depend on the magnitude of the range tested.

Overall ingestion, expressed in particles $\text{h}^{-1} \text{g}^{-1}$, appeared to be independent of seston quality. However, when ingestion was expressed in $\text{mg h}^{-1} \text{g}^{-1}$ it decreased with increasing food quality for all diet concentrations.

Cranford and Grant (1990) also found a decrease in ingestion rate with increasing food quality when adult *P. magellanicus* were fed diets of *C. gracilis*, Tahitian *Isochrysis*, and resuspended silt. The opposite trend for ingestion rate ($\text{mg h}^{-1} \text{g}^{-1}$) with increasing food quality has been found for these scallops than reported for blue mussels. For example, Bayne et al. (1989) found ingestion to increase with increasing seston quality when *M. edulis* were fed mixed algae and silt diets (0.8 to 7.4 mg l^{-1} , 18 to 71.0% POM). This observed difference in ingestion rates with varying food quality between sea scallops and blue mussels may be related to differences in feeding strategy. Mussels may be utilizing a "maximal rate strategy" whereas scallops may be using an "affectable rate strategy" (Jorgenson 1990, Ward et al. 1992). With a few exceptions there appears to be very little obvious difference in feeding activity between sea scallops and other species of bivalves studied under similar circumstances.

4.3. Estimating Energy Losses

4.3.1. Faeces Production and Absorption Efficiency

The percent POM in the faeces ranged from a mean of only 17 to 24% for all experimental diets. A seasonal range of 19 to 39% has been observed for adult *P. magellanicus* fed

natural seston in eastern Newfoundland (R.J. Thompson, personal communication). Organic content of the faeces was independent of seston concentration (Figure 10A), and increased slightly then plateaued with increasing seston POM (Figure 10B). This is very significant because it suggests that sea scallops extract POM from their food supply down to an almost constant level before expelling the faeces regardless of the initial concentration or level of POM in the diet. It has been previously thought that absorption efficiency in bivalves is greatly reduced when they are fed high concentrations of food rich in POM (e.g. Widdows et al. 1979).

Absorption efficiency has been corrected for any possible selection of organic over PIM through the production of pseudofaeces. Pseudofaeces was produced in 10 of the 12 diet mixtures and showed significant percent enhancement in five out of the above 10 diets. However the absorption efficiency was only slightly changed in the 7-25, 3-80 and 14-80 diets (Table 11). Overall, particle selection by juvenile sea scallops through the production of pseudofaeces did not routinely alter the estimate of absorption efficiency. However, in a few experiments it was altered, and if not taken into consideration could underestimate the amount of material absorbed using the standard Conover ratio.

The 80 % POM C. muelleri scallop absorption efficiencies in Table 23 compare favourably to absorption efficiencies for adult bay scallops (range = 78.1 to 89.9 %) fed three different algal species (Pierson 1983). Bricelj and Kuenstner (1989) found absorption efficiencies as high as 89.7 % for the bay scallop fed T. weissflogii (concentration = 1.2 to 12×10^3 cells ml^{-1}) using the twin ^{14}C ^{51}Cr radiotracer method. Scallop absorption at the 25 % POM and 50% POM mixtures in my study had a broader range, between 16.6 and 73.7%, than efficiencies recorded (range = 53 to 63 %) for M. edulis fed a wider range of POM (POM 17.7 to 71.0 %) consisting of mixed suspensions of algae and silt (Bayne et al. 1989). Finally, Bricelj and Malouf (1984) found a mean absorption efficiency of 22.5 % for diets of low POM (ca. 13-15 % POM, 0-44 mg l^{-1} silt), whereas pure algal diets of P. paradoxa (ca. 0.62 mg l^{-1} algae) were absorbed with 82 % efficiency. There was a clear trend of increasing absorption efficiency with increasing diet quality, with values recorded for the 25% diets most likely to represent values in the natural environment. It should therefore be possible to predict absorption efficiency for this species by evaluating the quality of the seston.

The trend of increasing absorption efficiency with better seston quality in this study agrees with Cranford and

Grant (1990), who found absorption efficiency increased with increasing food organic content for adult *P. magellanicus* fed sediment diets (ca. 20 to 45 % POM) over a narrow range of concentrations (0.5 to 2.5 mg l⁻¹). Vahl (1980) found a strong relationship between POM and absorption efficiency for the Icelandic scallop, *Chlamys islandica*, with absorption efficiency increasing with higher fractions of organic matter in natural seston. The hard clam has also displayed an increase in absorption efficiency with increasing food quality (Bricelj and Malouf 1984). Conflicting results have been reported for *M. edulis*. There was no change in absorption efficiency with seston quality for blue mussels over a range of mixed suspensions of algae and silt (0.8 to 7.4 mg l⁻¹, 17.7 to 71.0 % POM (Bayne et al. 1989). However, earlier reports showed it to increase with increasing seston quality between 9.2 and 35.8 % POM (6.8 to 110.9 mg l⁻¹) (Bayne et al. 1987).

Both corrected and uncorrected absorption efficiencies were independent of seston concentration. This is very different from earlier results reported for bivalves fed algal diets. Absorption efficiency has been found to decrease with increasing algal concentration for bay scallops (Bricelj and Kuenstner 1989), surf clams (Möhlenberg and Kierboe 1981) and the blue mussel (Thompson

and Bayne 1974, Foster-Smith 1975, Widdows 1978, Bayne and Newell 1983). However, at natural seston concentrations, no decrease in absorption efficiency for *M. edulis* has been observed with increasing seston concentration (ca. 10-100 mg l⁻¹) (Bayne and Widdows 1978) and at mixed suspensions of algae and silt (0.79-7.43 mg l⁻¹, 17.7-71.0 %POM) (Bayne et al. 1989).

My results agree with Bayne et al. (1989) and Bayne and Widdows (1978). A reason for this may include the fact that the diet mixtures did not consist solely of algal cells but also inorganic particles. Other reasons might be that particle concentrations similar to natural levels were used and the bivalves were exposed to the experimental diet for several days prior to measurements being recorded. Absorption efficiency is functionally related to gut capacity, gut residence time and ingestion rate (Bayne and Newell 1983). Thus absorption efficiency is more likely to be a function of the ingested ration rather than the ambient food concentration. If a bivalve can adjust its CR or the production of pseudofaeces to maintain a constant ingestion rate, the food consumed is likely to be absorbed with equal efficiency at low or high particle loads.

4.3.2. Oxygen Consumption

Oxygen consumption was independent of both seston concentration and seston quality for all diet mixtures (range = 0.22 to 0.34 ml O₂ h⁻¹ g⁻¹, Table 13, Figures 12A-B). These rates are in agreement with seasonal changes in oxygen consumption reported by Vahl (1978) for C. islandica (range ca. 0.10 to 0.25 ml O₂ h⁻¹ g⁻¹, temperature = 1-8° C) fed natural seston. MacKay and Shumway (1980) found similar rates for the deep water scallop, C. delicatula, (= 0.38 ml O₂ h⁻¹ g⁻¹, temp. = 10° C) as did McKlusky (1973) with the queen scallop, C. opercularis, at 10° C of 0.38 ml O₂ h⁻¹ g⁻¹ (acclimated to temperature for 1 week) and 0.23 ml O₂ h⁻¹ g⁻¹ (acclimated to temperature for 5 weeks). Adult P. magellanicus has shown oxygen consumption rates of 0.34 ml O₂ h⁻¹ g⁻¹ when fed natural seston (temp. = 10-12° C) in eastern Newfoundland at a depth of 10 m (MacDonald and Thompson 1986) and rates of 0.22 ml O₂ h⁻¹ g⁻¹ at 10° C (Shumway et al. 1988). Rates for these scallops are similar to published values for other species.

Oxygen consumption, a good indicator of metabolic rate in bivalves, is functionally related to filtration rate or CR (Griffiths and Griffiths 1987). Increases in feeding activity include not only increases in the energy expended on actual propulsion of water through the mantle cavity, but

also the physiological cost involved in the processing and digestion of the ingested ration (Griffiths and Griffiths 1987). Bayne and Scullard (1977) found filtration rates and oxygen consumption in M. edulis to increase dramatically when they were presented with food. It is interesting that scallops in my study maintained constant metabolic rates despite the reduction in CRs as concentration increased.

C. delicatula fed algae (P. lutheri, concentration of 30,000 cells ml^{-1}) did not respond by increasing oxygen consumption significantly (Mackay and Shumway 1980). These authors suggested that species that normally feed discontinuously (e.g. intertidal mussels) may respond to changes in food supply, in terms of their respiration rate, more noticeably than species that feed continuously (i.e. sublittoral scallops). McKlusky (1973) found that the addition of food (D. euchlora, concentration of 8,000 to 10,000 cells ml^{-1}) during an experiment did not increase oxygen consumption in the queen scallop. M. edulis has been shown not to change its oxygen consumption rate with increasing food concentration at natural seston ranges of 6.77-110 mg l^{-1} , 9.2-35.8 % POM (Bayne et al. 1987), nor at natural seston ranges of 0.79-7.43 mg l^{-1} , 17.7-71.0 % POM (Bayne et al. 1989). Oxygen consumption is independent of particle concentration for surf clams fed mixed suspensions

of *P. tricornutum* (0-0.5 mg l⁻¹) and suspended bottom material (0-25 mg l⁻¹, Møhlenberg and Kiørboe 1981). However, oxygen consumption was found to decrease with large increases in suspended sediments (0-2000 mg l⁻¹) for the soft shelled clam, *Mya arenaria* (Grant and Thorpe 1991). Oxygen consumption in sea scallops was independent of seston concentration and quality like many of the bivalves previously studied.

4.3.3. Ammonia Excretion

Ammonia excretion in this study was independent of both seston quantity and quality (range = 17.9 to 34.6 $\mu\text{g NH}_4\text{-N h}^{-1} \text{ g}^{-1}$) and comparable to other published values. Bayne et al. (1987) found little change in non-weight specific ammonia excretion rate in *M. edulis* (range = 61.6 to 212.8 $\mu\text{g NH}_4\text{-N h}^{-1}$) fed natural seston (6.8 to 110.9 mg l⁻¹, 9.2 to 35.8 % POM). Widdows and Johnson (1988) also observed little change in ammonia excretion for blue mussels (range = 14.6 to 20.5 $\mu\text{g NH}_4\text{-N h}^{-1} \text{ g}^{-1}$) exposed to low concentrations of natural seston (= 0.70 mg l⁻¹, 39 % POM) and low concentrations of aromatic hydrocarbons (= 0.003 to 0.031 mg l⁻¹). Bayne and Scullard (1977) found that ammonia excretion (non-weight specific) decreased over a 17 day period (from 33 to 15 $\mu\text{g NH}_4\text{-N h}^{-1}$ at 11° C) in *M. edulis* fed mixed algal

suspensions of *P. tricornutum* and *T. suecica*. Soft shell clams exposed to 0.0018 mg l^{-1} *Tetraselmis* sp. did not change their ammonia excretion rate with time (range = 25.3 to $30.8 \text{ } \mu\text{g NH}_4\text{-N h}^{-1}$) whereas the experimental clams exposed to $100\text{--}200 \text{ mg l}^{-1}$ intertidal sediment (duration 5 weeks) did show an increase in excretion with time (28.0 to $51.8 \text{ } \mu\text{g NH}_4\text{-N h}^{-1}$) (Grant and Thorpe 1991).

Studies that measure oxygen consumption and ammonia excretion together have shown that these two rates may vary independently, indicating that ammonia excretion is not simply a function of overall metabolic activity (Griffiths and Griffiths 1987).

The energy lost through excretion may only represent a small portion of the total energy budget. For example, approximately 1 to 10 % of the total energy is lost for *M. edulis* and less than 5% for *P. magellanicus* (Bayne and Newell 1983, Thompson 1984). Energy lost to ammonia excretion expressed as a percentage of total energy absorbed (0.63 to 6.26 % total routine absorbed and 0.58 to 3.33 % of total active absorbed) for scallops in this study compared closely to those reported for adult scallops in Newfoundland. These values were calculated from mean maximum and minimum ingestion rates and mean maximum and minimum ammonia excretion rates from Figures 9A-B and Table 23,

respectively. Ammonia excretion then, for P. magellanicus in the present study, did not represent a significant loss of energy.

4.4. Integration of energy gain and losses- Scope for Growth

To estimate the range of values of scope for growth (SFG) as accurately as possible, it was decided to use both active and routine CRs to calculate an active SFG and a routine SFG. It was thought that routine CRs (includes zero values) may underestimate true absorption and therefore true SFG while active rates (all zero values omitted) may overestimate SFG. The true SFG probably lies somewhere between these two estimates. The identical values of respiratory and excretory losses were used to calculate both active and routine SFG. Any observed differences in SFG are due solely to differences in CRs which are often variable and can be somewhat difficult to measure consistently.

Active SFG ranged from 2.1 to 69.0 J h⁻¹ g⁻¹ while routine scope for growth ranged from 1.3 to 56.3 J h⁻¹ g⁻¹ (Table 15). MacDonald and Thompson (1986) reported SFG in adult P. magellanicus in eastern Newfoundland feeding on natural seston. Values were expressed in kJ g⁻¹ month⁻¹ and converted to J h⁻¹ g⁻¹ by converting the values to Joules and

hours (assuming a 30 day month). SFG for a 5 g scallop were lowest in the winter, often approaching zero, and highest in August, when values reached $6.60 \text{ J h}^{-1} \text{ g}^{-1}$ at 12° C . Much higher values were recorded in my study than observed in the natural environment because the experimental scallops were fed very high concentrations of pure cultured algae that had a much higher energy content than natural seston.

Similar seasonal values (range -2.1 to $+70.8 \text{ J h}^{-1} \text{ g}^{-1}$) have been found for the Icelandic scallop, C. islandica, at temperatures between 3 and 4.5° C , seston concentrations between 3 and 13 mg l^{-1} , and POM from 20 to 60% (Vahl 1980). M. edulis in eastern Newfoundland displayed a range of 8.3 to 25.0 J h^{-1} , for temperatures between 0 and 15° C , seston concentrations from 2 to 7 mg l^{-1} , and 25 to 50% POM (Thompson 1984).

Scope for growth (active and routine) for scallops in my study increased with increasing seston concentration. The typical trend for bivalve scope for growth, from short term laboratory experiments with unicellular algal cultures at low rations, is that scope may initially be negative at very low concentrations, increase to a peak and then level off (Griffiths and Griffiths 1987). This trend was reported in the seasonal studies by the above authors and has also been found for laboratory studies with M. edulis fed natural

seston. Bayne et al. (1989) recorded scope for growth values between 6 and 13.5 J h⁻¹ when blue mussels were exposed to concentrations between 0.79 and 7.43 mg l⁻¹ with percent organic matter ranging from 17.7 to 71.0 %. Scope for growth increased at a reducing rate for the same species (-6.17 to +15.58 J h⁻¹ g⁻¹) fed mixed concentration of algae and silt (0 to 1.4 mg l⁻¹) at 10 ° C (Widdows 1978). Stuart (1982) found a similar trend for the blue mussel fed D. primolecta (0.3 to 5.0 J h⁻¹) and aged kelp detritus (3 to 45 J h⁻¹ at concentrations between 0.5 and 6.0 mg l⁻¹). The trend seen in my study agrees with other published reports.

Both active and routine SFG for juvenile sea scallops increased with increasing seston quality for all diets (Table 15). There were no negative mean values of SFG during the experiments. Bayne et al. (1989) found no variation in scope for growth in M. edulis with increasing seston quality (when expressed a fraction of the inorganic portion of the food (% POM)), but found it to increase at a decreasing rate with increasing amount of POM (when expressed as mg POM l⁻¹). Grant and Cranford (1991) calculated carbon and nitrogen scope for growth as a function of diet in P. magellanicus when exposed to four separate diets (i.e. C. gracilis, ca. 78 % POM; Tahitian Isochrysis, ca. 82 % POM; aged kelp, ca. 90 % POM; resuspended sediment, 30 % POM). They observed an

increase in scope for growth with increasing food quality. My results agreed with Grant and Cranford (1991).

Scope for growth is often measured in short term laboratory studies to predict the response of the animal to a variety of conditions in the natural environment. There has been reasonable agreement between growth predicted from physiological measurements (scope for growth) and growth determined directly (e.g. Dame 1972, Bayne and Worrall 1980, Grant and Cranford 1991). More recently, some authors have examined bivalve physiological response, SFG, and realized growth under somewhat more realistic conditions by using seston consisting of mixed algae, detritus, inorganic silt and or resuspended sediment (Murken 1975; Winter 1976, 1978; Kjørboe et al. 1980, 1981; Stuart 1982, Bricelj and Malouf 1984, Bricelj et al. 1984, Robinson et al. 1984, Bayne et al. 1987, 1989; Cranford and Grant 1990, Grant and Cranford 1991, Grant and Thorpe 1991).

The addition of small amounts of bottom sediments (5 to 10 mg l⁻¹) to bivalve diets accelerates growth rates in blue mussels by as much as 30-70 % (Winter 1978, Kjørboe et al. 1981). However, the addition of silt to experimental diets did not enhance growth in hard clams (0 to 44 mg l⁻¹) and caused starvation in soft-shell clams (100-200 mg l⁻¹) (Bricelj et al. 1984, Grant and Thorpe 1991). Grant and

Cranford (1991) examined the carbon and nitrogen scope for growth in adult *P. magellanicus* exposed to diets such as kelp detritus, phytoplankton and resuspended sediment and found that, depending on the physiological state (O:N ratio) of the sea scallop, sediment and kelp detritus could enhance phytoplankton diets, but could not act as sole food sources. Finally, the addition of kaolinite (clay) to a supplemented diet of algae, yeast and rice starch fed to *C. virginica* has resulted in greatly improved growth, comparable to that of oysters fed on a 100 % algae ration (Urban and Langdon 1984). The food costs of culturing juvenile oysters could be reduced by 56 % using a 50 % algal ration supplemented with yeast, rice starch and kaolinite instead of using algae alone (Urban and Langdon 1984).

P. magellanicus in the present study appeared to show no relative difference in scope for growth at concentrations greater than 3 mg l⁻¹ when fed a 50% organic mix of algae and silica versus a ration consisting of 80% POM (i.e. 100% algae). A direct grow out experiment with both ration mixtures (50 and 80 % POM) would be required to confirm that scallops could grow as effectively on a 50% diet as they could on an 80% diet. If this is true it may have implications for the cost effectiveness of rearing algae and

the hatchery/nursery stage of culturing this species of scallop.

4.5. Scallop Conditioning Experiment

Few studies have examined the potential effects of previous conditions or the length of time bivalves are held before physiological measurements are taken. Bivalves are often starved for a standard period of time to reduce variability associated with individuals collected from different environmental conditions. Bayne et al. (1987) measured physiological activity in blue mussels held two days and compared it to rates for mussels held two weeks. In one mussel population they found much higher SFG after two weeks than after two days due to increases in clearance, and absorption efficiency and reduced metabolic expenses associated with respiration.

Unlike previously mentioned experiments evaluating acclimation period my conditioning experiment was designed to test whether there was a significant effect associated with the length of time I held scallops before measurements were taken. Clearance, ingestion and absorption efficiency often became independent of time after between 24 and 72 hs of exposure to the diet. Therefore, as long as scallops were exposed to the experimental diets for at least 24 hs, enabling them to adjust their feeding rates to the new

conditions, there should be no bias associated with making the physiological measurements over a three day period. For example, during the first 24 hs scallops were exposed to the diets before measurement of oxygen consumption on Day 2. The same scallops were continuously exposed to the diet for another 24 hs before measurement of clearance on Day 3, bringing the total exposure to 48 hs. This continued for an additional 24 hs before measurement of excretion on Day 4, resulting in a total conditioning period of 72 hs.

When exposed to a 3 mg l⁻¹ 80 % POM diet of C. muelleri the scallops continuously fed algae prior to measurements (supplemented group) displayed significantly higher CRs, pseudofaeces production rates and ingestion rates compared to their counterparts fed only background seston (maintained group).

4.6. Scallop Feeding Strategy

Foster-Smith (1975, 1976) has observed that when suspension feeding bivalves are exposed to increasing suspended particle loads, they are able to control or regulate the total amount of material ingested by: a) reducing the time spent pumping (discontinuous feeding behaviour), b) reducing their CRs, and/or c) increasing the amount of material rejected in pseudofaeces. I have found

that juvenile *P. magellanicus*, when exposed to increasing particle loads in a laboratory environment (at 12° C), are able to regulate their ingestion rate by reducing their CR and increasing the amount of material rejected in pseudofaeces, in order to maintain a high absorption efficiency. An increase in SFG with particle concentration is facilitated by maintaining relatively constant oxygen consumption and ammonia excretion rates.

4.7. Conclusions.

Juvenile sea scallops, *P. magellanicus*, were exposed to laboratory diets that mimic the range of seston conditions this species encounters in the natural environment in eastern Newfoundland (i.e. concentrations 2-15 mg l⁻¹ and organic composition 20-50% depending on the season; MacDonald and Thompson 1986). Changes in feeding activity and physiological responses were evaluated using techniques of physiological energetics. To accomplish this, scallops were fed diets (at 12° C) of set quantity and quality (i.e. 25%, 50% and 80% organic content and particle concentrations \approx 1, 3, 7, and 14 mg l⁻¹) using the microalgal diatom *C. muelleri* (POM) and inert silica (SiO₂; PIM). Scallops were fed 12 diets in all, 3 different qualities for each of the four concentrations. The following responses and trends were observed.

1) Sea scallop CR decreased with increasing concentration between 1 and 3 mg l⁻¹ and then became appeared to become independent of particle concentration between 3 and 14 mg l⁻¹. CRs were highest at the poorest quality diet (25% POM) and lowest at the highest quality diet (80% POM), a trend indicating that this species needs to clear more of the poor quality diet per unit time to

obtain amounts of energy similar to those obtained from a better quality diet.

2) Pseudofaeces (part. $h^{-1} g^{-1}$) produced in 10 out of the 12 diets, increased with increasing seston concentration and was lowest at the 50 % POM diets. Notably, pseudofaeces was produced by scallops fed relatively low concentrations of food (i.e. 1 mg l^{-1} diets representing ≈ 8000 part. ml^{-1}). Pseudofaeces production did not, however, represent a large proportion of the total material cleared (i.e. 7.2% maximum in part. $h^{-1} g^{-1}$ and 32% maximum in mg $h^{-1} g^{-1}$).

3) The percentage of POM in all pseudofaeces samples was compared to levels of POM in the representative diets to determine whether scallops were preferentially rejecting inorganic particles. Significant percent enhancement (percentage of diet enhanced above or below the percent POM of the diet) was found in 5 out of the 10 diet mixtures. Positive enhancement was found for scallops fed 50% and 80% POM diets, while scallops fed the highest concentration and lowest quality (i.e. 14-25) diet mixture reduced the quality of the material to be ingested. If significant enhancement occurred, positive or negative, it was measured to make the appropriate correction to the ingested ration before calculating the scallop's absorption efficiency.

4) Ingestion rates, in part. $\text{h}^{-1} \text{g}^{-1}$, increased with increasing seston concentration and then appeared to plateau at seston concentrations greater than 7 mg l^{-1} . When expressed in $\text{mg h}^{-1} \text{g}^{-1}$, ingestion rate appeared to increase between 3 and 7 mg l^{-1} and then become independent of seston concentration between 7 and 14 mg l^{-1} . Overall, ingestion, expressed in part. $\text{h}^{-1} \text{g}^{-1}$, appeared independent of seston quality, while ingestion rate ($\text{mg h}^{-1} \text{g}^{-1}$) clearly decreased with increasing food quality for all diet concentrations. With few exceptions there appeared to be little obvious difference in feeding activity between sea scallops and other species of bivalves studied under similar conditions.

5) Faeces percent POM ranged only from a mean of 17% to 24% for all experimental diets. With the exception of the results from the 25% organic levels, the organic content of the faeces was independent of both seston quantity and quality. This is significant because it suggests that sea scallops can extract POM from their food supply down to an almost constant level before expelling the faeces regardless of the initial concentration or level of POM in the food supply.

6) Absorption efficiency was corrected for any possible selection of POM over PIM through the production of pseudofaeces. Overall, particle selection by juvenile

scallops through the production of pseudofaeces did not greatly alter the estimate of absorption efficiency. If not taken into account, as was done in this thesis, particle selection could underestimate the amount of material absorbed using the standard Conover ratio. Absorption efficiency was found to be independent of seston concentration, and increased markedly with increasing seston quality for all diet mixtures. These scallops appeared to adjust their CRs or the production of pseudofaeces in such a way as to maintain constant ingestion rate, and consequently were able to absorb food with equal efficiency at low or high particle loads.

7) Oxygen consumption was independent of both seston concentration and seston quality for all diet mixtures. This allowed the scallops to maintain relatively constant metabolic rates despite the reduction in clearance as concentration increased.

8) Ammonia excretion was also independent of both seston concentration and quality for all experimental diet mixtures and did not represent a significant loss of energy (i.e. less than 7% lost to ammonia excretion expressed as percentage of the total energy absorbed).

9) Once all of the energy gains and losses were converted to energy equivalents ($\text{Joules h}^{-1} \text{g}^{-1}$), the

potential energy available for growth and gamete production (referred to as Scope for growth) could be determined. Scope for growth for all scallops in my study increased with increasing seston concentration and quality.

10) P. magellanicus showed no apparent difference in scope for growth at concentrations greater than 3 mg l^{-1} when fed a 50% organic mixture of algae and silica compared to a ration consisting of 80% POM (i.e. 100% algae). A direct grow out experiment with both ration mixtures (50 and 80% POM) would be required to confirm that scallops would grow as effectively on a 50% organic diet as on a 80% organic diet. If this were true, it would have implications for the effectiveness of rearing algae and the hatchery/nursery stage of culturing this species of scallop. If algae could be supplemented with silica or other relatively inexpensive inorganic particles, perhaps the cost of growing expensive algae could be reduced.

11) A scallop conditioning experiment was conducted to test the effects of pre-acclimation and the acclimation time before physiological measurements are taken. When P. magellanicus was exposed to a 3 mg l^{-1} 80% organic diet of C. muelleri for 72 hours the scallop's CR, ingestion rate and absorption efficiency often became independent of time between 24 and 72 hours of exposure to the diet. Hence as

long as scallops were exposed to the experimental diets for at least 24 hours, enabling them to adjust their feeding rates to the new conditions, there should be no bias associated with making physiological measurements over a 3 day period. Also, scallops fed algae (supplemented group) prior to measurements displayed significantly higher clearance rates, pseudofaeces production rates and ingestion rates compared to their counterparts fed only background seston (maintained group).

12) Juvenile sea scallops, when exposed to increasing particle loads in a laboratory environment (at 12° C), are able to regulate their ingestion rate by reducing their CRs and increasing the amount of material rejected in pseudofaeces in order to maintain a high absorption efficiency. An increase in scope for growth with particle concentration is facilitated by relatively constant oxygen consumption and ammonia excretion rates.

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Appendix A

A.1. Experimental diet mixtures

Appendix Table A.1: Chaetoceros muelleri weight determination with percent POM (ash free dry weight) included **

Number of particles on 2.5 cm filter	N	Mean weight algal cells (blank subtracted) (mg) \pm s.d.*	Mean weight of individual algal cell (mg)	Mean weight of individual algal cell (pg cell ⁻¹)
5.7993 $\times 10^6$	6	0.352 \pm 0.281	6.070 $\times 10^{-8}$	60.70
15.4648 $\times 10^6$	6	1.184 \pm 0.413	7.656 $\times 10^{-8}$	76.56
30.9296 $\times 10^6$	6	1.601 \pm 0.254	5.176 $\times 10^{-8}$	51.76
48.3275 $\times 10^6$	6	2.703 \pm 0.474	5.593 $\times 10^{-8}$	<u>55.93</u>
				Mean = 61.24 \pm 10.85

* Mean blank = 0.737 \pm 0.130 mg (N = 6)** The mean percent POM of C. muelleri = 78.3 \pm 17.2 (%), N = 12

Appendix Table A.2.: Silica weight and POM determination

Two attempts were made at determining the weight of the silica dioxide used in my diet mixtures. The weight of individual silica particles was initially estimated at a mean of $103.00 \text{ pg} \pm 6.35$ and POM of 0.8 ± 0.5 (%), $N = 36$. Two initial feeding experiments were conducted based on this weight and percent POM. However, the observed weights of the diet mixtures were much higher than had been calculated. For example, a 1 mg l^{-1} 25 % and a 3 mg l^{-1} 25 % diet mixture were aimed for, but instead the diets actual observed weights and POMs were 2.5 mg l^{-1} 27 % POM and 10 mg l^{-1} 8 % POM.

This known, using these two diet weights, the actual mean weight of the individual silica particles were back calculated and the mean weight of the individual silica particles for these two diets was found to be 220 and 312 pg part.^{-1} respectively. The Grand mean of these two recalculated diets was 270 pg part.^{-1} . This final weight of a silica particle of $270 \text{ pg part.}^{-1}$ was used from then on for all 12 of my diet calculations.

Appendix Table A.3. Calculation of inorganic and organic content of diet mixtures

1) Calculation of a 1mg l⁻¹ 25 % POM (particulate organic material) and 75 % PIM (particulate inorganic material) diet. G. Mueller is 78.3 % organic, not 100 % organic. Therefore, to obtain a 1 mg l⁻¹ seston sample at 25 % POM and 75 % PIM, 0.32 mg l⁻¹ would contain algae and 0.68 mg l⁻¹ would contain silica (i.e., 100/78.3 = 1.27 x 0.25 mg l⁻¹ = 0.32 mg l⁻¹ of algae). The following indicates how the number of partic. ml⁻¹ for a 1 mg l⁻¹ 25 % organic diet was calculated:

$$\begin{aligned} & 75 \% \text{ PIM} = 0.68 \text{ mg l}^{-1} \text{ silica} \\ & (\text{silica} = 270 \text{ pg partic.}^{-1}) \end{aligned}$$

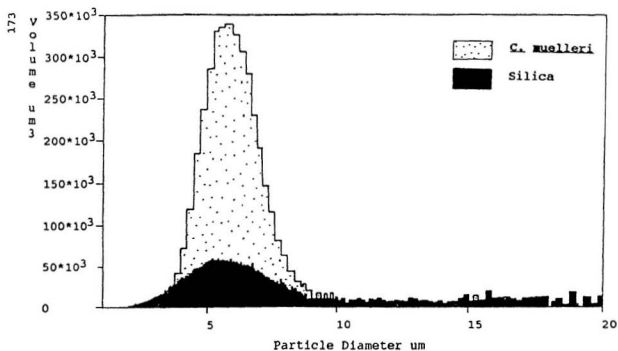
$$\begin{aligned} & 25 \% \text{ POM} = 0.32 \text{ mg l}^{-1} \text{ algae} \\ & (\text{algae} = 61.24 \text{ pg partic.}^{-1}) \end{aligned}$$

# partic. l ⁻¹ =	0.68 mg l ⁻¹ 270 pg partic. ⁻¹	# partic. l ⁻¹ =	0.32 mg l ⁻¹ 61.24 pg partic. ⁻¹
=	$\frac{6.8 \times 10^{-4} \text{ g l}^{-1}}{2.70 \times 10^{-6} \text{ g partic.}^{-1}}$	=	$\frac{3.2 \times 10^{-4} \text{ g l}^{-1}}{6.124 \times 10^{-6} \text{ g partic.}^{-1}}$
=	$2.5185 \times 10^5 \text{ partic. l}^{-1}$	=	$5.225 \times 10^4 \text{ partic. l}^{-1}$
=	$2.5185 \times 10^5 \text{ partic. ml}^{-1}$	=	$5.225 \times 10^4 \text{ partic. ml}^{-1}$

2) For the 50 % POM and 50 % PIM diet mixture a 1 mg l⁻¹ diet required 0.635 mg l⁻¹ of algae and 0.365 mg l⁻¹ of silica (i.e., 100/78.3 = 1.27 x 0.50 mg l⁻¹ = 0.635 mg l⁻¹ of algae). The number of particulates ml⁻¹ required to forcementenforced particulates to equal a 1 mg l⁻¹ 50/50 PIM/POM mixture as calculated above were: 1.352 x 10⁵ partic. ml⁻¹ for silica and 1.037 x 10⁵ partic. ml⁻¹ for the G. Mueller.

3) For the 80 % POM and 20 % PIM diet mixture only G. Mueller was used therefore in a 1 mg l⁻¹ sample 0.783 mg l⁻¹ was algae. The number of particulates ml⁻¹ required to equal a 1 mg l⁻¹ 20/80 PIM/POM mixture as calculated above was: 1.633 x 10⁴ partic. ml⁻¹.

4) The above values in partic. ml⁻¹ for each organic ratio were multiplied by 3, 7 and 14 to obtain the higher concentration diets.



Appendix B

Appendix Figure B.1. Particle size distributions of *C. muelleri* and silica dioxide (particle volume (μm^3) versus particle diameter (μm)).

Appendix C

Appendix Table C.1.: Mixing bucket test to determine if equal volumes of diet were delivered to all scallop containers.

Bucket hose number	Flow rate (mls min. ⁻¹)	Mean particle count (part. ml ⁻¹) (N = 3) ± s.d.
1	41	1571 ± 31.0
2	42	1646 ± 27.0
3	42	1569 ± 34.0
4	47	1596 ± 3.6
5	41	1582 ± 28.9
6	46	1606 ± 18.6
7	48	1597 ± 5.5
8	47	1608 ± 14.7
9	45	1615 ± 35.5
10	42	1591 ± 37.8
11	50	1661 ± 34.6
12	41	1617 ± 24.9
13	40	1634 ± 23.6
14	43	1613 ± 1.1
15	49	1529 ± 9.5
16	43	1612 ± 33.5

C.2. Determining rate of flow in the flow-through apparatus

An important underlying assumption in estimating clearance rates of bivalves from the removal of particles in a flowing system, is that each volume of water passes through the filtration organs only once. In other words, the exhalant water must not mix with the inhalant water. If a bivalve recirculates the passing suspension and thus dilutes the concentration of particles in the inflowing water a serious underestimation of clearance rates can occur (Hildreth and Crisp 1976, Riisgard 1977). The rate of flow over the animals must be sufficiently high to prevent any recirculation. Above a critical flow, the measured clearance rates are representative of the bivalve's actual clearance rates. Consequently, a preliminary experiment was conducted to determine the critical flow rate through the scallop holding containers of the flow through apparatus.

Scallops in the same approximate size range as those for my 12 experiments were used (shell height between 50 and 55 mm). Six scallops were velcroed to the bottom of one container each with the excurrent portion of the mantle positioned next to the drain (see Section 2.2.1.4.) Two containers were left empty serving as the controls. Three of the six scallops were selected to have the flow rate changed with time to six different rates (50, 65, 108, 177, 207 and 260 mls min.⁻¹) The remaining three were kept at 50 mls min.⁻¹ during the experiment. A diet of C. muelleri ($\approx 1 \times 10^4$ cells ml⁻¹) was fed to the scallops during the experiment. All scallops were acclimated to the apparatus and diet concentration for 24 hours prior to the experiment at 50 mls min.⁻¹. The time of the experiment was five hours in duration. At time 0: a water

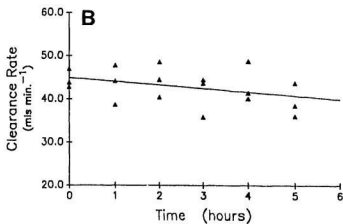
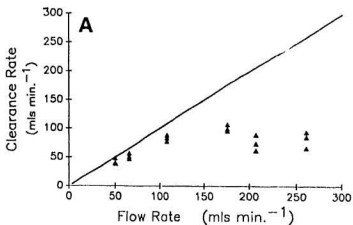
collection was taken from each container and the controls and the particle concentration in all containers were determined by a Coulter Multisizer (Model II) fitted with a 100 μm tube. The flow rate in three scallop containers and a control was then changed to 65 mls min.⁻¹. Scallops were allowed one hour acclimation to this flow rate and then water collections were taken from all eight containers, the particle concentrations were determined and the flow rate on three of the containers was changed to the next higher rate. This procedure was continued until collections were made for the flow rate of 260 mls min.⁻¹ (hour number 5). All clearance rates were determined as in Section 2.2.1.4.

Clearance rate (mls min.⁻¹) as a function of the flow rate (mls min.⁻¹) is shown in Figure C.2.A., where the line for clearance = flow rate is also shown. Clearance rate values approach this line when flow rates are low (≈ 50 mls min.⁻¹). Above a certain flow rate the clearance values deflect from the line and tend to form a plateau (i.e. Flow rate > 130 mls min.⁻¹). The clearance rate becomes independent of flow rate in this range, > 130 mls min.⁻¹, and recirculation of the water becomes insignificant.

The control scallops, with flow rates held constant over the experimental period, showed no change in clearance rate with time ($b = -0.8255$, $r^2 = 0.03658$) (Figure C.2.B.). Therefore time was not considered a variable that influenced clearance rate during this experiment. Based on the above results the clearance rates chosen for my feeding experiments were between 150 and 180 mls min.⁻¹ because clearance rate was found to be independent of flow rate in this range.

Appendix Figure C.2.A. Clearance rate (mls min⁻¹) of scallops in flow rate experiment versus water flow rate (mls min⁻¹). The line represents $Y = X$.

C.2.B. Clearance rate (mls min⁻¹) of scallops with flow rates held constant in flow rate experiment versus water flow rate (mls min⁻¹).



Appendix Table D.1: CHN seston quality

Experimental diet mixture (mg l ⁻¹ organics)	N,N	POC* (mg dry wt. seston ⁻¹) ± s.d.	PON* (mg dry wt. seston ⁻¹) ± s.d.
125	3,3	7.72 ± 3.00	0.57 ± 0.06
325	3,3	17.06 ± 4.17	7.78 ± 9.12
725	1,1	12.12 ± N/A	8.15 ± N/A
1425	3,3	6.00 ± 1.41	0.26 ± 0.10
150	3,3	20.55 ± 1.21	10.75 ± 6.30
350	2,2	18.01 ± 1.40	8.90 ± 8.62
750	3,3	13.20 ± 1.22	0.10 ± 0.10
1450	3,3	8.52 ± 0.75	1.31 ± 0.57
180	2,2	27.70 ± 0.42	3.89 ± 0.12
380	3,2	22.40 ± 3.45	3.51 ± 0.71
780	1,1	14.14 ± N/A	1.71 ± N/A
1480	3,3	22.14 ± 0.55	3.64 ± 1.39
380**	3,3	22.78 ± 1.67	4.75 ± 2.33

* Particulate Organic Carbon and Nitrogen

** Scallop Conditioning Experiment seston results.

